Technical Report No. 21

THIRD PROGRESS REPORT AND BUDGET PROPOSAL FOR FY 74 AND FY 75

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ISLAND ECOSYSTEMS IRP

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ABSTRACT

This document is the third annual progress report of the ISLAND ECOSYSTEMS STABILITY AND EVOLUTION Subprogram of the U. S. International Biological Program (IBP). It covers the period from February 1972 through February 1973.

During this third year, the Subprogram has moved towards further integration in accordance with the synthesis aims of IBP. Our ten areas of research activity (detailed in Tech. Rpt. #2:18-19) have been consolidated into four synthesis themes. These are:

(1) SPATIAL DISTRIBUTION OF ISLAND BIOTA
(2) TEMPORAL PHENOMENA IN ISLAND ECOSYSTEMS
(3) NICHE DIFFERENTIATION IN ISLAND ECOSYSTEMS
(4) GENETIC VARIATION OF ISLAND SPECIES IN RELATION TO ENVIRONMENT

The coordinators of these synthesis themes are identified as the section editors of the respective chapters (2 through 5) in this report. Our organizational structure remains essentially the same as shown on p. 20 of the previous annual report (Tech. Rpt. #2). Dr. Kent Bridges joined our program in August 1972 as Assistant Director and Modeller replacing Dr. M. P. Mi in the latter function.

This report previews the synthesis attempts of our program in chapters 2 through 5. In addition, it gives information on the status of each individual subproject (Chapter 6). Further activity results are shown by the abstracts of 18 new Technical Reports that were written during this year (Chapter 7), by 21 contributions submitted for publication in scientific journals and by the list of 30 theses and dissertations supported through our program (Chapter 8).

We intend to make the writing of our synthesis volume a primary activity starting January 1974 so that the manuscript may be ready by June 1974, the official termination date of IBP. However, in June 1974 our program will have only been in operation for 3-3/4 years. We intend to pursue our integrated research aims over the entire 5-year period as originally anticipated. Our plans for continuing beyond the IBP deadline are outlined in the introduction.

BUDGET ENDORSEMENT

In accordance with the phase-over plans beyond the IBP deadline, we are submitting our budget for the two remaining years of our 5-year program, FY 74 and FY 75. The budget request for FY 74 (September 1, 1973 to August 31, 1974) amounts to $473,950 and that for FY 75 (September 1, 1974 to August 31, 1975) to $459,407.

We request that these sums be made available in two separate institutional grants -- one to the University of Hawaii, the other to the Bishop Museum -- as detailed at the end of this report (Chapter 9).

Respectfully submitted,

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TABLE OF CONTENTS

	Page
ABSTRACT	i
BUDGET ENDORSEMENT	ii
1. INTRODUCTION	1.1-1.3
Synthesis plans for IBP	1.1
Continuation plans beyond IBP	1.1
2. SPATIAL DISTRIBUTION OF ISLAND BIOTA	2.1-2.7
Ecological amplitudes	2.1
Hypotheses of species distribution	2.3
Experimental design and sampling	2.4
Progress of data analysis	2.7
3. TEMPORAL RELATIONS IN ISLAND ECOSYSTEMS	3.1-3.7
Rhythmic and cyclic phenomena	3.1
Structural relationships	3.1
Evolutionary relationships	3.2
Current status of this research	3.3
Successional phenomena	3.3
Replacement by exotic species	3.3
Recovery trends of native species	3.4
Succession on new volcanic surfaces	3.4
Recovery following experimental herbivore displacement	3.5
4. NICHE DIFFERENTIATION IN ISLAND ECOSYSTEMS	4.1-4.6
Community structure	4.2
The nature of habitat utilization by all avian species in the community	4.2
Gradient analysis of avian community structure in relation to plant community structure	4.2
Consumer relations	4.3

Page

5. GENETIC VARIATION WITHIN ISLAND SPECIES IN RELATION TO ENVIRONMENT 5.1-5.5

The usefulness of insular species 5.1

Speciating organisms: are they the dynamic element in island ecosystems? 5.2

Microevolution within species 5.2

The genetics of recent introductions 5.3

Genetic changes in populations of endemics from Kilauea Forest 5.4

Non-speciating organisms: are they relatively stable elements in island ecosystems? 5.4

6. PROGRESS OF SUBPROJECTS 6.1-6.59

B-1 Vegetation-environment correlation studies 6.1

B-2 Studies of plant to plant interactions: studies of distributional dynamics 6.4

B-3 Progress report of phenological and growth studies, 1972 . 6.5

B-4 Life history studies of important plants: Angiosperms . . . 6.7

B-5 Progress report on fern study (Cibotium spp., the Hawaiian tree ferns) 6.9

B-6 Progress report on genecological studies of Metrosideros . 6.10

B-7 Progress report on the ecological role of soil algae . . . 6.11

B-8 Progress report on the roles of fungi in island ecosystems. 6.13

B-8 Progress report on the occurrence and ecological roles of soil fungi associated with Acacia koa on the Mauna Loa Transect 6.17

C-1 Biosystematics of Hawaiian Diptera: Diptera fauna in native forest litter-distribution, abundance and factors responsible for variation 6.21

C-2 Progress report on the ecology of Hawaiian Sciaridae . . . 6.22

C-3 Progress report on cerambycid-borer study 6.23

C-4 Progress report on phytophagous insects - sap and seed feeders (Heteroptera) 6.26

C-5 Progress report on effects of sap-sucking Homoptera on Hawaiian ecosystems 6.29

Page

C-6 Progress report on faunal research on Metrosideros 6.31

C-9 Progress reports on soil and duff inhabiting arthropods, vertebrate ectoparasites, and cavernicoles in lava tubes . . 6.35

C-11 Progress report on insect interference in the reproductive cycle of community structure-forming plants, particularly seed feeders 6.41

C-12 Progress report on effects of diseases of insects in Hawaiian ecosystems 6.42

D-1 Progress report: Life history and evolution of Hawaiian honeycreepers 6.44

D-1 Progress report on gradient analysis of the avian community 6.46

D-2 Progress report on small mammals 6.48

D-3 Progress report on the physiological ecology of some terrestrial Hawaiian birds and mammals 6.49

E-1 Progress report on genetic variations of Hawaiian Drosophila immigrans 6.53

E-1 Continuing studies on Hawaiian Drosophila species 6.55

E-1 Preliminary report on electrophoretic variation in Acacia koa 6.58

E-2 Progress report on data processing 6.59

7. TECHNICAL REPORT SERIES AND ABSTRACTS 7.1-7.10

8. LIST OF CONTRIBUTIONS AND THESES 8.1-8.4

ISLAND ECOSYSTEMS IRP/IBP HAWAII Contribution Numbers 1-23 . . . 8.1

Theses prepared under partial support of the US/IBP ISLAND ECOSYSTEMS IRP 8.3

9. BUDGET FOR FY 74 and FY 75 . . . . . 9.1-9.49

Proposed IBP Grant Budget, 04 year 9.1

Proposed IBP Grant Budget, 05 year 9.26

10. LITERATURE CITED 10.1-10.3

1. INTRODUCTION

1.1 - 1.3

D. Mueller-Dombois

1. INTRODUCTION

The ISLAND ECOSYSTEMS Integrated Research Program (IRP) was launched effectively on September 1, 1970. Thus, as of March 1, 1973 -- the time of writing of this report -- the program has been in operation for 2½ years. A first progress report and budget renewal was written in December 1970 (Technical Report #1, 144 pp.). A second progress report and budget renewal was written in January 1972, after 1½ years of work (Technical Report #2, 290 pp.). From its initiation, the program was planned as a 5-year project. This would set its termination date as August 31, 1975.

The present progress report reviews the period since January 1972, and the budget proposal covers the remaining two years, FY 74 (from September 1, 1973 through August 31, 1974) and FY 75 (from September 1, 1974 through August 31, 1975).

Since our program is a part of the U.S. contribution to the International Biological Program (IBP), we are also cognizant of the official termination date of IBP, which is one year prior to our anticipated completion date. The IBP schedule forces us into a synthesis phase already at this time. Thus, we have made plans for synthesis of our research to be completed by June 1974, the official termination of IBP. But we also have plans for continuing our research beyond IBP to at least August 1975, i.e., the 5-year period as originally anticipated for our program.

Synthesis plans for IBP

In accordance with our four objectives which were detailed by several working hypotheses in our originally funded proposal (of February 1970), we plan to synthesize our research results under four main integrated themes. These are:

(1) Spatial distribution of island biota.
(2) Temporal phenomena in island ecosystems including rhythmic and cyclic as well as successional trends.
(3) Niche differentiation in island ecosystems in terms of analysis of functional species groups. This will include analysis of community structure and consumer relations.
(4) Genetic variation within island species in relation to environment.

The four themes are planned as the main chapters of a synthesis volume integrating the results of our program. Our annual review symposium (November 10, 1972) was already structured into these four themes. Similarly, in the present report, we are attempting a preview of our synthesis by a discussion of the four themes.

Plans are made to begin writing the synthesis volume a year from now so that a first manuscript will be ready by June 1974.

Continuation plans beyond IBP

Our IBP synthesis will relate to studies on two main IBP sites, the Mauna

Loa Transect (see Technical Report #2: 22, Fig. 2) and the Kilauea Forest Reserve (see Technical Report #1: 59 and Technical Report #2: 52). Integrated field work on these two sites will essentially be completed by September 1973. Data sets for synthesis, either in the form of individual Technical Reports or in the form to be ready for computer analysis, are expected to be ready in December 1973 so that writing of the synthesis chapters can begin in January 1974.

While the coordinators and chapter editors of the four synthesis themes are occupied with data analysis and writing during the spring semester of 1974, we intend to continue with validation studies along the Mauna Kea Transect (Technical Report #2: 22, Fig. 7).

An altitudinal transect comparison was an essential part of our original research design. We intend to use the fifth year of our operation (FY 75) to carry this plan to completion. For this reason, our FY 75 budget proposal (in this report) does not differ much from our FY 74 budget. During both years, FY 74 and FY 75, field work will continue, but at a somewhat reduced level. Field trips involving validation studies along the Mauna Kea Transect will be more expensive than in Hawaii Volcanoes National Park because we lack housing facilities in the Mauna Kea area. However, since the number of trips will be fewer, travel expenses will be approximately the same.

Although not yet accounted for in this budget proposal, our future intentions are to compare the relatively young (about 1000-year old) montane rain forest biome (i.e., the Kilauea Forest Reserve) with a geologically much older (about 5 million-year old) montane rain forest biome (on the island of Kauai). Here we can find several of the same species and species complexes as in the geologically young rain forest biome. However, since the age difference is so great, we can expect evolutionary changes within the same species complexes. For example, some of the major community-structure forming species complexes are the same, such as the tree genus Metrosideros and the tree fern genus Cibotium. But their quantitative relations differ considerably. We may also find that these taxa are genetically different. An ecosystem comparison of this sort, whereby we can hold the climate and biogeographic relations relatively constant, but vary the geological age, will permit us to really get down to the problem of ecosystem evolution. This approach of using the island age sequence as an experimental design for field research was emphasized in our original proposal. We intend to apply this design after we have completed the detailed ground work that was necessary to begin our island ecosystems studies under IBP.

Beyond the age-comparison of ecosystems in the same biogeographic region (i.e., the Hawaiian Islands), we intend to compare our island transects with those along similar altitudinal climatic gradients, but in different biogeographic regions. The first target comparison is planned for New Guinea, where the Bishop Museum maintains the WAU Ecology Institute (see Technical Report #2: 10).

Thus, our concept to continue island ecosystems research beyond the termination of IBP follows a plan that was presented already in the original proposal (of February 1970) and was further developed in Technical Report #2. Our research management objectives are to complete certain well-defined targets together as a

research team. At the same time, we see these targets merely as steps in a broader framework of island ecosystems analysis.

A summary of the proposed time schedule for synthesis and continuation of our research is shown in Table 1.

Table 1. ISLAND ECOSYSTEMS IRP schedule of current and continuing activities with target dates.

Activity	Target date
(1) Completion of field work on two IBP sites (M. Loa TR & Kilauea Forest Reserve)	September 1973
(2) Individual data analysis, processing and interpretation (i.e., Tech. Rpts.)	December 1973
(3) Synthesis of data sets and writing of synthesis volume chapters	June 1974
(4) Field work on validation sites (Mauna Kea Transect)	August 1975
(5) Completion of 5-year project, incorporation of validation results in a revised synthesis volume	Fall 1976
(6) Continuation of island ecosystems research in the form of rain forest biome comparison on geologically old island	After August 1975
(7) Comparison of tropical island transects in different biogeographic regions (e.g., New Guinea) but as controlled by similar altitudinal climates	Following or contemporaneously with the within-Hawaiian Islands comparison. A new 5-year program, 1975-1980.

2. SPATIAL DISTRIBUTION OF ISLAND BIOTA

2.1 - 2.7

D. Mueller-Dombois

2. SPATIAL DISTRIBUTION OF ISLAND BIOTA

Ecological amplitudes

In contrast to most tropical continental vegetations, the native forest vegetation of the Hawaiian Islands is remarkably simple. There are, in fact, only two dominant, tall-growing (25-30 m maximum) native tree species, Metrosideros collina (with several varieties) and Acacia koa (with few varieties). These are wide ranging dominants whose spatial distribution can be ecologically characterized as follows (FIG. 1):

On the most southern Island Hawaii (the so-called "Big Island" with an area of 4,038 square miles), Metrosideros ranges from sea level to 8,200 feet (2,500 m) elevation on Mauna Loa (13,677 feet = 4,170 m). In terms of climatic parameters this means that the tree grows in a year-round warm-tropical climate of 23°C mean air temperature all the way up into a cool-tropical, high-altitude climate of 8°C mean air temperature. The upper boundary of Metrosideros is marked approximately by the year-round nocturnal ground-frost boundary (Mueller-Dombois 1967). Acacia koa has a more limited range on Mauna Loa from 4,000-6,700 feet (1,220-2,043 m), overlapping with Metrosideros. On Mauna Kea (13,796 feet = 4,206 m) and on the island of Maui, Acacia koa occurs in a similar high altitude range as on Mauna Loa, but it also occurs in the lower montane belt together with Metrosideros. On the islands of Oahu and Kauai, Acacia koa only occurs below the range of Metrosideros, and the two species rarely form mixed stands. However, a few widely scattered or rare Metrosideros individuals of shrub-stature do occur down to 500 feet (150 m) on Oahu and to sea level on Kauai.

The change in range of these species is correlated with substrate age. Mauna Loa is still an active volcano whose currently exposed lava rock substrate ages range from probably post-pleistocene to present. In contrast, most of the Mauna Kea surfaces are from late pleistocene (from 600,000 to about 15,000 years ago). The substrates on Oahu and Kauai are from 1-6 million years old (Macdonald and Abbott 1970). The substrate age effect is primarily one of changing soil water regimes, from xeric to hydromorphic, in the mid-elevation rain forest range. The dying Metrosideros in the wet areas on the older substrates is often correlated with poor drainage. However, correlation with substrate age and soil moisture regime does not mean that those factors are also the causes of these distributions. The causes are as yet unknown.

Several other native woody life forms of small-tree or shrub stature have similarly wide-ranging (but often interrupted) distributions, for example, the trees Myoporum sandwicense, Sophora chrysophylla and the shrub Styphelia tameiameia (which may be split into low (S. tameiameia) and high elevation (S. douglasii) species). Other species of similar life form have peculiarly narrow ranges. Such species may belong, however, to wide ranging genera, such as the shrub Cyrtandra, which apparently occurs with 118 species on Oahu (St. John 1966), an indication that this taxon has been fractioned by adaptive radiation. These fractioned taxa are responsible for another ecological peculiarity, found mostly on the older volcanic islands, namely that physically similar habitats may be occupied by quite dissimilar communities in terms of species composition. Thus, the pattern of

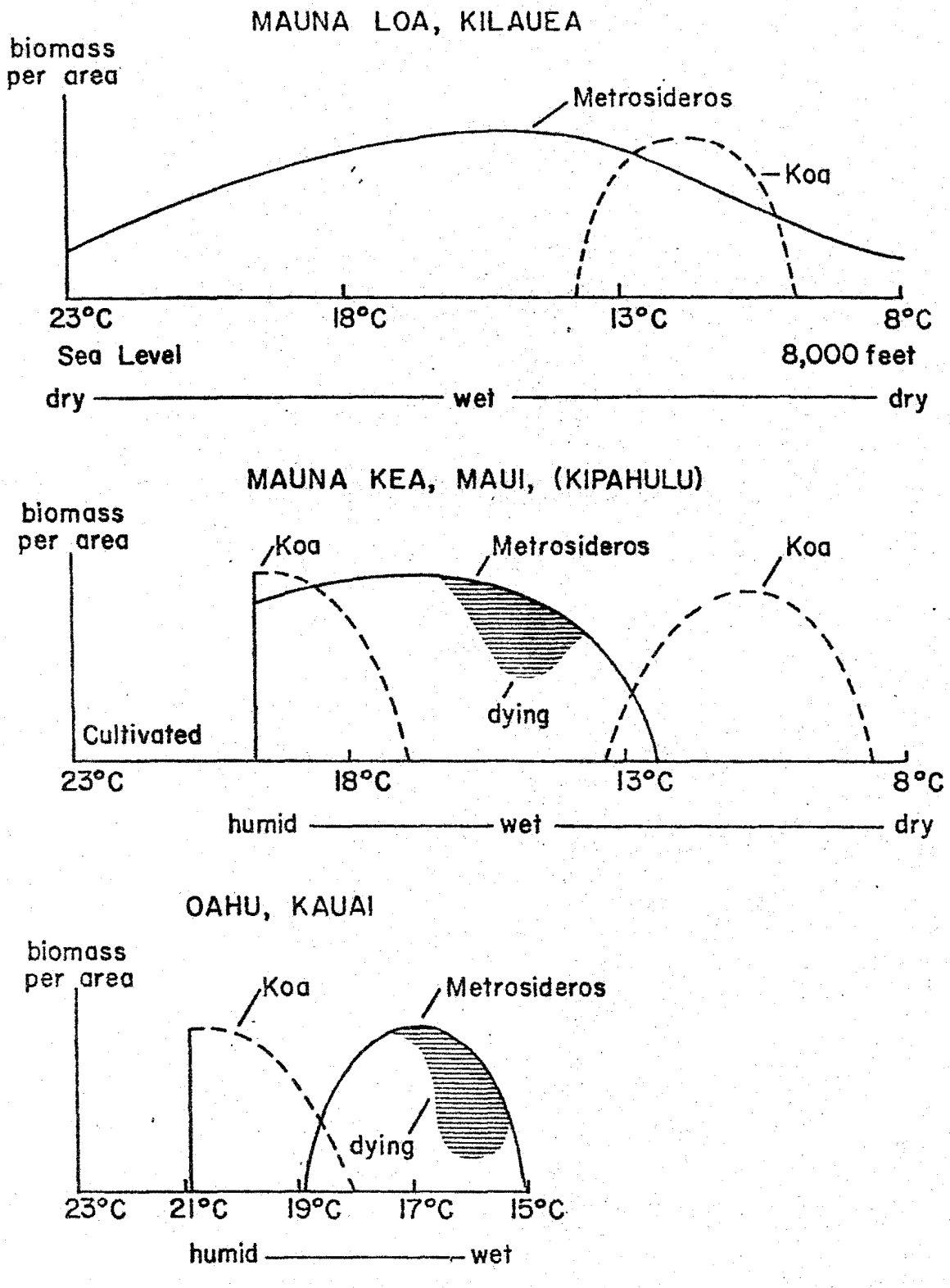


FIG. 1. General ecological amplitudes of the two most important native tree species (Metrosideros collina and Acacia koa) in the mountainous Hawaiian Islands.

recurrence of similar species combinations in similar habitats varies between islands and generally decreases with island age.

Hypotheses of species distribution

Based on a working hypothesis that endemic birds, insects and other subsidiary life forms evolved primarily in adaptation to the community-structure forming dominant native plant species, we are testing the degree of spatial association of native biota along environmental gradients. Our current test gradient is a 22 mile-long transect on the east flank of Mauna Loa, which cuts through 12 structurally well-defined vegetation types, i.e.,from alpine scrub to Metrosideros-Cibotium (tree fern) rain forest, from 10,000 feet (3,049 m) to 4,000 feet (1,220 m) elevations. Both tree species, Metrosideros collina and Acacia koa, form the structural dominants in these ecosystems, and we are trying to find out specifically whether native ecosystem stability is here related to the biomass (as defined by density and height) of these two major native tree species. As an initial index of native ecosystem stability we will use the proportion of native and exotic population sizes within life form groups of an ecosystem, realizing, however, that stability involves persistence over time in the presence of certain disrupting forces or perturbations.

So far, this hypothesis appears to be supported by the distribution study of phytophagous insects (Gagné 1972), but not, for example, by the soil arthropods (Radovsky 1972). In the former group many endemic species are found where these two tree species are most vigorous, while among the soil arthropods most species are exotics. The latter show wide distributions, quite unrelated to the vigor or distributional variations of the native tree species and ecosystems.

There are currently four hypotheses about species and community distribution along environmental gradients. These have recently been stated by Whittaker in his 1970 textbook (Whittaker 1970: 35) as follows:

1. "Competing [dominant] species exclude one another along sharp boundaries. Other species evolve toward close association with the dominants and toward adaptation for living with one another." (This species distribution would result in distinct zones.)

2. "Competing [dominant] species exclude one another along sharp boundaries, but [other species] do not become organized into groups with parallel distributions." (This would result in zones with overlapping species ranges.)

3. "Competition does not [usually] result in sharp boundaries [i.e., zonation] between species populations. Evolution of species toward adaptation to one another will, however, result in the appearance of groups of species with similar distribution." (This would result in a pattern of typical communities separated by ecotones.)

4. "Competition does not usually result in sharp boundaries between species populations, and evolution to one another does not result in the formation of groups with similar distributions. Instead, centers and boundaries of species populations are scattered along environmental gradients." (This

would result in no recognizable zonation and absence of typical communities.)

All of the four spatial distribution patterns seem to be possible. Whittaker's studies in continental temperate mountain ecosystems supported the last named hypothesis. Our studies in island tropical mountain ecosystem seem to support the third hypothesis as far as the native biota are concerned.

Moreover, Whittaker (1970) holds that the highest degree of integration is accomplished by a high beta-diversity. High beta-diversity implies accomodation of a large number of species with restricted distributions along a given environmental gradient as opposed to a few wide-ranging species on the same gradient. Low beta-diversity appears to be a characteristic along altitudinal gradients on oceanic islands, at least in Hawaii. In the tropics, this is a peculiarity only for islands. Whether this also means poor integration, needs further examination. An increase of beta-diversity through exotic species invasions appears to show the opposite, namely a decrease in integration.

Experimental design and sampling

From the beginning our research group was oriented and agreed on two sampling ideas:

(a) Participants were to work with related species groups rather than with individual species.

(b) These were to be sampled in previously defined ecosystems along altitudinal transects.

The species groups and respective investigators were fitted into an organizational model (February 1970 Proposal: 29, Fig. 15 and Tech. Rpt. #2: 217) to indicate their general functional relationships within an ecosystem context. An overall objective was to study the specific ecological roles of these biota groups on our study sites. This aspect is further discussed in Chapter 4 of this report.

The transect approach seemed useful for a number of reasons. An important one was that sampling results could be related to two major known environmental variables: temperature and rainfall. The questions that offered themselves through this sampling design were: How are island species and species groups organized spatially in relation to (a) the major environmental parameters, and (b) to one another --across the several ecosystems that we encounter along the Mauna Loa Transect (our first chosen transect, Tech. Rpt. #2: 22, Fig. 2).

Part (a) can be answered independently for each biota group. Part (b) requires integrated sampling in a number of "focal" sites along the Mauna Loa Transect.

During an IBP field meeting in August 1972, we decided as a team that each transect investigator will sample his organism group in a minimum of 14 identical locations along the Mauna Loa Transect. The common locations were those where a majority of the investigators had already sampled prior to this decision. The 14 so-called focal IBP transect sites are briefly described in TABLE 2.

TABLE 2: Focal IBP Sites on Mauna Loa Transect (Transect-Profile No.1, Tech. Rpt. #2, p. 24)

IBP site No.	Location and elevation	Vegetation	Transect Segment
1	Thurston Lava Tube 3,920 ft.	Closed ohia-tree fern forest	12
2	Sulphur Bank 4,000 ft.	Open ohia-matted fern (Dicranopteris) forest	11
3	Tree Molds area 4,000 ft.	Open ohia-native shrub-lichen forest	10
4	Kipuka Ki near climatic station, 4,200 ft.	Koa-Sapindus savanna	8
5	Power Line Trail 4,920 ft.	Mt. Parkland, koa colony	7
6	IBP Climatic Station 5,250 ft.	Mt. Parkland, koa colony	7
7	Keamoku Flow, just above 5,650 ft.	Mt. Parkland, koa colony	7
8	Above Goat Exclosure 6,200 ft.	Mt. Parkland, koa colony	7
9	End of Strip Road 6,700 ft.	Mt. Parkland, koa colony (uppermost)	7 to 6 transition
10	7,000 foot level	Subalpine scrub with scattered trees	6
11	7,500 foot level	Subalpine scrub with scattered ohia trees	6 to 5 transition
12	8,000 foot level	tree line ecosystem	5
13	9,000 foot level	very scattered low alpine scrub	3
14	10,000 foot level Puu Ulaula area	very scattered low alpine scrub	3 to 2 transition

Note: Decrease in mean annual air temperature from IBP site 1 to 14, from 16°C - 8°C.
Decrease in mean annual rainfall from IBP site 1 to 14, from 2500 mm - 750 mm.

In addition, we developed a hierarchial sampling concept in relation to the size and general environmental sensitivity or behavior of our respective organism groups. On this basis, we recognized three sampling groups:

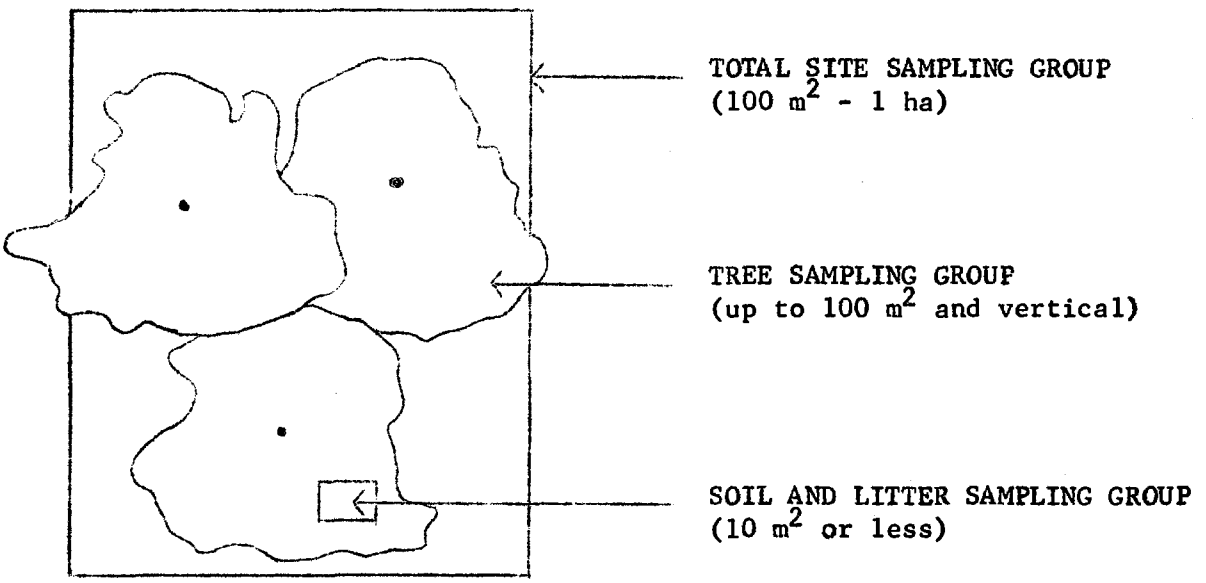
1. SOIL AND LITTER SAMPLING GROUP
   Baker-Meeker-Stoner (fungi B-8)
   Doty (soil algae B-7)
   Radovsky-Howarth (soil arthropods C-9)
   Delfinado-Hardy (litter inhabiting Diptera C-1)

2. TREE SAMPLING GROUP
   Gagné (phytophagous insects, Heteroptera C-4)
   Nishida-Haramoto-Nakahara (Metrosideros insects C-6)
   Beardsley-Leeper (sap-sucking insects, Homoptera C-5)
   Gressitt-Davis (Cerambycid bark and stem beetles C-3)

3. TOTAL SITE SAMPLING GROUP
   M. Dombois-Spatz (vascular plants B-1)
   Tomich (rodents D-2)
   Berger-Conant (birds D-1)
   Steffan (Sciaridae C-2)
   Paik (exotic Drosophila E-1)
   Carson (endemic Drosophila A-1)

Because our sampling levels are hierarchical in size, sampling group 1 is accomodated within the sampling range of group 2 and group 2 in that of group 3. The basis for this is to attain a reasonable homogeneity across the three sampling levels so that group 1 sampling is meaningful in the framework of group 2 sampling and group 2 sampling is meaningful in the framework of group 3 sampling. Following is a sketch to illustrate what is meant by hierarchical integrated sampling.

A SAMPLING SITE



Progress of data analysis

Data sets for each organism group are now prepared for computer analysis. A two-way table was programmed as computer printout in which all species are listed in their respective life-form groups on the left side in one column. The table head shows the 14 transect sites in an altitudinal sequence. The table body itself contains the quantitative values obtained for each species. In this way, species amplitudes across the altitudinal transect are shown together with their spatially varying quantitative importance. In several following steps, certain new species groups are identified that have similar distributional trends across the altitudinal gradient. The table is then rearranged accordingly.

The distributional organization in space along the gradient will then provide information on:

(a) What groupings of biota we may mathematically designate as communities.
(b) What organisms and how many we may single out as demonstrating co-existence and possibly coadaptation and to what degree.
(c) What are the alpha-diversity changes upslope in relation to environment. This will be shown within and across life-form groups and also with regard to species origin (i.e., endemic, introduced, cosmopolitan, etc.).
(d) What is the degree of beta-diversity in young island ecosystems (i.e., how many species within the life-form groups studied are packed along a given spatial climatic change).

These analysis questions (a-d)lend themselves to comparisons with continental gradient studies. From such comparisons we may draw conclusions about island ecosystems stability (in terms of life form and species diversity differences) and evolution (in terms of the organizational stage of island community evolution).

3. TEMPORAL RELATIONS IN ISLAND ECOSYSTEMS

3.1 - 3.7

K. Bridges
D. Mueller-Dombois

TEMPORAL RELATIONS IN ISLAND ECOSYSTEMS

Rhythmic and cyclic phenomena

The role of an organism in an ecosystem often changes during the course of a year. For some plant species, the period during which they have flowers present makes them available for different utilization than during the non-flowering period. Insects which are diapausing certainly have a different impact on their food sources than when they are active. These examples illustrate that the functional role of an organism is not determined simply by its presence or abundance, nor is the structure of an ecosystem adequately described only by listing the various species present. Specification of the timing of the phenological states of the organisms occurring within a site is prerequisite to an adequate description of the structure and functioning of that ecosystem.

In order to investigate this aspect of ecosystems, it is necessary that we recognize that the organisms progress through a series of distinguishable stages (or phenophases). This sequence of phenophases is generally repeated, in some cases by an individual and in others by a population, resulting in a rhythmic or cyclic phenomenon. Although we often associate this sequence with a yearly-time base, this is not always the situation.

There are both structural and evolutionary aspects of this synthesis study which make it particularly relevant to island ecosystems. The structural role, for example, of the many timing mechanisms of continental ecosystems are likely to be either less intense or lacking in corresponding island ecosystems. This is particularly true of the annual-temperature variation when the climate of the island ecosystem is buffered by the surrounding ocean. Ecosystems in the tropics are also lacking the large changes in daily radiation throughout the year that are such a prominent feature of temperate ecosystems. The Hawaiian Island Ecosystems research sites share both these attributes.

Evolutionary hypotheses regarding rhythmic phenomena may be proposed at several levels of biological organization. For example, has there been selection such that the individuals of a species population display synchrony of phenophase transitions? This has implications regarding the size of a population required to sustain a species population. At a higher level of organization, it may be asked whether there has been selection for specific timing relationships between different species either in mutualistic or competitive relationships. As in the structural-relationships synthesis, the comparison of island and continental ecosystems should help clarify the theories of rhythmic phenomena.

The remainder of this synthesis overview will discuss the structural and evolutionary problems of rhythmic phenomena in greater detail and provide a preliminary indication of what Island Ecosystems subprojects are providing data to examine these problems.

Structural relationships. - There has been considerable attention given to the life-history aspects of many organisms when they are viewed as species populations. When analyzed quantitatively, this information generally results in a developmental history of a species expressed as continuous functions for some life-history aspects for the entire life span of the individuals comprising the

population. These functions generally take the form of survivorship and birth-rate curves (see Allee, et al. 1949). Vertebrate populations have often been described in this manner, with no attempt to divide the population into discrete phases. The developmental history is more likely to be divided into discrete phases when insects are used (for example, Read and Ashford 1968). The concept of rhythmic phenomena as used in this synthesis requires the division of the developmental life histories into discrete phases and the determination of the factors responsible for controlling the rate of the progression of the phenophases. This procedure simplifies the study of the relationships of organisms to each other as complicated by phenophase synchrony. While both forms of life-history analysis have utility, there will be emphasis placed on using discrete life-history phases. There are several mechanisms involved in determining the rate of phenophase progression. These mechanisms need not be entirely exclusive. The length of a phase may be determined by a relatively internal (=intrinsic) timing mechanism, as with the 'day-degree' control of the length of the instars of many insects. This timing is based on an 'accumulation' whose rate is continuously varied, at least by small amounts, following small changes in the environment. Another type of mechanism uses environmental factors as triggers (or cues) which result in the transition from one phenophase to another. In this case, the factors which trigger the transition are not necessarily involved in determining the length of the succeeding phase. Rainfall which exceeds a threshold amount has been used successfully as such a trigger for phenophase transitions in modelling arid vegetation (Bridges, et al. 1972); the timing of some tropical insects appears to be based on rainfall and hours of bright sunlight (Leston 1972).

An analysis of the rhythmic phenomena which will result in the definition of life-history patterns will yield an integrated synthesis at several levels of biological organization; the relationships between a species population and its environment, the relationship between two different species populations, and the organization of communities. For example, if an individual species population is to persist in an area without periodic reinvasion, there must be sufficient mechanisms operating to allow the population to cycle through its life-history sufficiently rapidly and often enough to maintain the population. For an individual species existing in a marginal habitat, there may be a problem of maintaining sufficient propagative potential if rare environmental phenomena are utilized as triggers to initiate reproduction.

Some individual species populations cannot exist independent of the timing of other species populations. This is particularly apparent where herbivores feed on the flowers or nectar of periodically flowering plants or in some host specific predator-prey relationships.

The organization of a community is often strongly influenced by its patterns of temporal organization. There have even been attempts to classify communities based on this criterion (Stanyakovich 1970).

Evolutionary relationships. - The life-history strategies of species populations provide an interesting base for the analysis of the evolutionary aspects of community organization. For example, is it possible for one species to be able to 'escape' tight linkages with its predator? The 13 and 17 year cicadas are a classic use of an adaptive strategy by which a prime number cycle length does not allow submultiple cycle lengths. Yet the cycle length need not be this

exotic. In some oaks and conifers, for example, the two-year delay between the environmental trigger and the maturation of the seeds (Janzen 1971) may be adequate to keep insects from developing a population synchronous with their host.

The evolutionary aspects of rhythmic phenomena are of particular interest in understanding island ecosystems. The differences in the mechanisms and roles of rhythmic patterns of the endemic versus introduced species are expected to be particularly interesting.

Current status of this research. - There have been numerous reviews of cyclic phenomena (such as the synthesis volume sponsored by the US/IBP Phenology Committee, in press) and there are some theoretical studies on the timing of phenological events (see Cohen 1967 and Cohen 1970). There are few studies, however which have attempted to produce comprehensive theories which explain the species interactions and community aspects of cyclic phenomena. These synthesis studies generally relate to topics which incidentally include timing considerations (such as the seed predation review by Janzen 1971).

A majority of the Island Ecosystems subprojects will provide data for the interpretation of rhythmic phenomena. These are primarily concerned with direct investigation of structural aspects of life-history phenomena at the individual-species and population-interaction levels.

The species-level studies are comprised of subprojects on plants (B-3, phenology studies; B-7, algae;B-5, ferns; and B-6, Metrosideros), insects (C-2, Sciaridae; C-3, Cerambycidae; and C-6, endemic insects), decomposers (B-8, fungi), and vertebrates (D-2, rodents). The species interaction studies include plant-plant interactions (B-4), honeycreepers and plant phenology (D-1), rodents and their parasites (C-9), disease in insects (C-12) and several insect/plant studies (C-3, wood boring cerambycids; C-4, phytophagous Heterotera; C-5, sap-sucking Homoptera; and C-11, seed predation).

Successional phenomena

Succession relates to a change in the biotic community on the same site that is directional rather than rhythmic, a change that once started from a perturbation of some sort, continues for a period of at least several years before the rate of change becomes non-measurable.

In island community succession, it is particularly the interaction of man-introduced (exotic) and native species that can bring about some important ecological consequences. Recently, we completed several studies on succession or their effects. Some of the results can be summarized under two subheadings:

(1) Replacement by exotic species
(2) Recovery trends of native species

Replacement by exotic species. - A closed perennial grassland occurs in the mountain parkland ecosystem on the east flank of Mauna Loa (4,500-6,700 feet or 1,370-2,040 m elevation). It has a simple composition of about 10 herbaceous species. The currently most dominant grasses are the native Deschampsia australis

and the European Holcus lanatus. The latter was first collected in 1903 (Whitney et al. 1939). During a detailed reconnaissance in 1965, it was noticed that Holcus lanatus appeared to be more common on areas that were scarified or dug-up by feral pigs (Mueller-Dombois 1967). From 1971-72 we did a detailed experimental study to determine whether pig-digging aided in the spread of the introduced grass (Spatz and Mueller-Dombois 1972b). We found that both grasses participated in the invasion of freshly scarified soil, but that the rate of invasion of Holcus exceeded that of Deschampsia considerably. For example, a place that contained about 60% Deschampsia and only 25% Holcus before ground disturbance, had after one year a plant cover of 30%, of which about 15% was Holcus and less than 5% was Deschampsia. Areas with no noticeable ground disturbance are still dominated by the native grass. Thus, it seems clear from this study that the invasion of the exotic Holcus lanatus is decidedly favored by pig-digging.

The general replacement of a formerly native grassland by an exotic grassland has perhaps no serious ecological consequences, unless a number of other native biota are also threatened. However, since the area is in a National Park where the policy is to preserve the native ecosystems in their natural state, an important value judgment is involved. This relates to the elimination of feral pigs from the Park area, because the pigs represent a new stress factor that did not exist during island ecosystem evolution.

Another example of grassland establishment seems to have more serious ecological consequences. An Eastern North American grass, Andropogon virginicus (broomsedge), was noticed on Oahu, Hawaii in 1932 (Rotar 1968). This grass spread, and today it forms the dominant herbaceous cover in all denuded lowland (up to about 800 feet or 250 m elevation) rain forest habitats on windward Oahu. The grass is clearly a fire-adapted bunchgrass that accumulates dead standing yellow foliage in a few years. In addition, it goes into dormancy during the winter months just when the rainfall increases on windward Oahu. At that time of the year, in particular, the broomsedge grass cover forms a straw like mulch that reduces evapotranspiration from the surface, and this is in an area where excess water is a problem. Transpiration rate studies have shown that the Andropogon grass cover removes only a fraction (about 20-25%) of the incoming rain water during the winter months, October through April (Mueller-Dombois 1972a). On the same habitat, evergreen trees remove considerably more water because they maintain a much greater quantity of active leaf material on a square meter basis (2.24 kg/m^2 green foliage for the trees versus 0.58 kg/m^2 green blades for the grass). The habitat shows considerable erosion and runoff, much of which can indirectly be attributed to the introduced grass.

The dominance of Andropogon is maintained by periodic accidental fires. Apparently no other grass is available locally that can compete with Andropogon. In a similar continental tropical ecosystem, the winter-dormant Andropogon would probably not have become established. Here, instead, a fire-adapted grass would have taken its place; one that would remain green during the season of higher rainfall. This applies, for example, to Cymbopogon nardus in the continental island of Ceylon.

Recovery trends of native species. (a) Succession on new volcanic surfaces. - Plant invasion and recovery after a volcanic eruption was studied for nine years in a rain forest location (Smathers and Mueller-Dombois 1972) on a number of new

volcanic habitats at the Kilauea Crater in Hawaii. Among other things, the rate and sequence of plant life form invasion was recorded. On a pahoehoe lava rock habitat, algae, mosses and ferns arrived in the first year after new surface deposition. Lichens arrived in the third year and seed plants in the fourth year. The seed plants, consisted of five species, four of these were native woody plants (Metrosideros collina seedlings, Vaccinium reticulatum, Dubautia scabra and Hedyotis centhranthoides), one was an exotic species (Lythrum maritimum). As time went on, the frequency of the four native seed plants increased more uniformly over the new surface, but they were always found in the rock crevices. The exotic species disappeared, but other exotics became established, grasses in particular (Paspalum conjugatum, P. dilatatum, Andropogon virginicus and Setaria geniculata). These remained only in a very restricted area in a moister microhabitat.

Next to an undisturbed rain forest, several exotic woody plants (Buddleja asiatica, Rubus rosaefolius and Rubus penetrans) advanced quickly onto an ash surface. The exotics became established mostly at the base of standing snags, where the moisture relations were more favorable. However, native woody seed plants also became established. After a few years, considerable mortality was observed among the exotic woody plants (Buddleja, in particular), but not among the native species. Moreover, some individuals of the exotic Rubus shrubs were encroached upon and then replaced by native shrubs (Dubautia scabra and Vaccinium reticulatum) indicating competitive replacement. Here exotic grass species also arrived, but they remained in moister microhabitats.

The results show that, in general, native pioneer species are better adapted to the new, edaphically extreme habitats. However, exotic species participate in primary succession. Particularly those exotics appear to be successful that receive little or no competition from native plants. For example, no pioneer grasses have evolved in the Hawaiian rain forest. Exotic grasses, therefore, fill a vacant niche in primary succession on lava and ash surfaces in rain forest climates.

(b) Recovery following experimental herbivore displacement. - The mammalian herbivore niche was not filled in the course of island evolution. However, several large herbivores were introduced to the islands by the Europeans. Among these, goats became particularly abundant on the Island of Hawaii, where they were introduced about 200 years ago.

Goat concentration centers occur in the seasonally dry climates in the mountain parkland ecosystem and the coastal lowland of Hawaii Volcanoes National Park. Within the last five years, several goat exclosures were established in these two areas. A 10 m by 100 m goat exclosure was built in the mountain parkland in 1968. The exclosure was established in the grassland adjacent to an Acacia koa (koa) stand. Koa reproduces in the mountain parkland from root suckers, while in the rain forest it reproduces primarily from seed.

In 1971, a quantitative analysis was made (Spatz and Mueller-Dombois 1972a). At that time, the exclosure was stocked with a dense sapling stand of koa suckers from 10 cm to 2 m tall, while hardly any suckers of this size occurred outside the exclosure. However, a very large number ($>3/m^2$) of small (<5 cm) herbaceous root suckers were found outside. A structural survey of koa was made throughout

the mountain parkland, and the general trend was similar to the outside-exclosure pattern; i.e., a large number of small herbaceous suckers, very few taller woody saplings. Among the few taller woody saplings, about 50% were girdled and defoliated, had broken stems, or were dead and still standing.

This result shows two things that may be of evolutionary significance:

(1) That koa has a tremendous capacity to resprout, when its small herbaceous suckers are browsed,

(2) That koa has no capacity to resprout when the woody saplings are girdled or broken from browsing.

The capacity to resprout from roots appears to be an adaptation to grow competitively within closed grassland. Sprouting may also be encouraged by grass burning or ash fall-out from volcanic explosions. Fire appears to be a natural stress factor in this island environment (Mueller-Dombois and Lamoureux 1967, Vogl 1969). However, the very dense resprouting after clipping of herbaceous suckers is undoubtedly a new response. When goats are displaced after heavy browsing, koa saplings grow in dense thickets in which each individual becomes exposed to high intraspecific competition.

In contrast, the inability of woody saplings to resprout or form new leaders shows that koa is not really well adapted to browsing pressure. In a woody vegetation where browsing is a long-established factor, as for example in the monsoon forest-scrub vegetation of Ceylon, nearly all tree species were observed to respond to browsing by formation of new branches (Mueller-Dombois 1972b).

In 1968 a similar goat exclosure was constructed in the coastal lowland, in a summer-drought climate with 800 mm rain fall. Here the vegetation was dominated by the exotic, pantropical annual grass, Eragrostis tenella. Within two years the plant cover changed completely. Perennial bunchgrasses (Sporobolus africanus, Rhynchelytrum repens) became established. Among these was Heteropogon contortus, a grass introduced long ago by the Hawaiians. Also, woody chamaephytes began to grow here (Waltheria indica, Indigofera suffruticosa and Cassia leschenaultiana). But most surprising was the appearance of a native legume vine, Canavalia kauensis, that was identified as a new endemic species (St. John 1972). In the third year Canavalia covered > 50% of the surface area in the exclosure (Mueller-Dombois and Spatz 1972). Currently, the exclosure vegetation is still in the chamaephyte-vine stage, and its future development is difficult to predict.

The remarkable fact is that a native species, never seen before in this area, could produce the dominant plant cover in spite of so many years of intensive goat grasing. Our current explanation is that the vine must have germinated and flourished in the general area from time-to-time in wet years which occur every 5-10 years. Periodic goat hunting, as practiced by the Park Service as control, may have aided in the survival of the vine. It is probable that several other native species have become extinct in the lowland grass area because their seed supply became exhausted from more or less continuous feeding of goats on shoots and seedlings.

However, both examples show that native plant recovery is at least in part

still possible, when the introduced stress factor is removed. The Park Service is now fencing large areas in the lowland in an effort to recreate at least a partially native Hawaiian ecosystem.

4. NICHE DIFFERENTIATION IN ISLAND ECOSYSTEMS

4.1 - 4.6

A. J. Berger
S. Conant
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4. NICHE DIFFERENTIATION IN ISLAND ECOSYSTEMS

Kendeigh (1961: 18) defined a community as "an aggregate of organisms which form a distinct ecological unit. Such a unit may be defined in terms of flora, of fauna, or both. The extent of a community is limited only by the requirement of a more or less uniform species composition. Since plant communities and animal communities occur together in the same habitat and have many interrelations, the one can scarcely be considered independently of the other. Together they make up the biotic community, and the biotic community along with its habitat is termed an ecosystem." This is a straight-forward and clear definition, but the study of ecosystems in Hawaii is complicated because of their large numbers: 30 different ecosystems have thus far been defined on the eastern flank of Mauna Loa alone.

The functional unit within Hawaiian ecosystems for many principal investigators is the ecological niche as defined by Odum (1971: 234) who states, "The ecological niche of an organism depends not only on where it lives but also on what it does (how it transforms energy, behaves, responds to and modifies its physical and biotic environment), and how it is constrained by other species." Milstead (1972) proposed that there is a "finite number of broad ecological niches" in any given type of biome and that the niches can be defined by comparing the biology of convergent animal forms on different continents. He noted, however, that "past natural history studies do not yield the detailed type of information needed to make such comparisons. Thus, we find, on the one hand, that the study of either organisms or niches actually involves consideration of every conceivable relationship between an organism and its niche (as well as to every other organism in the niche), and, on the other hand, that adequate information is not now available for comparing niches on different continents, or even on the same continent or large island group. Hubbell (1968), for example, wrote that "no complete inventory of a large island's plants and animals has ever been made,... . But even in an archipelago supposedly so well known as Hawaii, every intensive modern study of a group of native animals or plants not only turns up previously unknown species, sometimes in large numbers, but also often reveals unsuspected and sometimes surprising evolutionary and ecological phenomena." And, indeed, a number of new "surprising evolutionary and ecological phenomena" have been discovered since the initiation of field studies by the Hawaii subprogram during the summer of 1970.

It is our goal not only to obtain masses of new information about plants and animals but also to attempt to understand and to describe the "broad" or general ecological niches in the Hawaiian ecosystems. Specifically, we intend to define them in terms of the species they contain and the ecological roles that the species play in these general niches and in the ecosystems as a whole. Upon approaching this goal, we feel confident that principles, theories, and models will result that will be of use both in Hawaii and in other parts of the world, with special reference to world-wide environmental problems. We are not so naive as to believe, however, that a full understanding of Hawaiian ecosystems can be had at the end of the initial period of investigation (September 1970 to June 1974); a very good start can be made, and certain aspects of ecosystem analysis will be finished and papers prepared for publication.

The raw material from which niche analyses can be made includes such data

as the following: plant life form and stratification, diversity of both plants and animals, quantitative analysis of plants and animals, annual cycles of plants and animals, predatory-prey relationships, interactions of introduced and endemic plants and animals, description of niches, number of species in a given niche, determination of probably unfilled niches, and the factors related to either stability or fragility of the Hawaiian ecosystems. Data gathered on these subjects during the past two years of the subprogram have been distributed recently as Technical Reports or are now being analyzed and prepared for distribution. Continuing studies on the same subjects will be essential in order to verify preliminary data, to be alert to the possibility of cyclical patterns, and to expand studies as accumulated information indicates that it is desirable.

Following are two examples of initial approaches to the subject of niche differentiation.

Community structure

Data required for describing community structure in Hawaii are still being gathered. A detailed study of the biology and ecology of the Hawaiian honeycreepers is viewed as a profitable approach to the question. The ecology of all endemic land birds is poorly understood (Berger, Gressitt, and Mueller-Dombois 1969: 16-17). Recent studies conducted by investigators in the Island Ecosystems Stability and Evolution Subprogram of the IBP (see Technical Report No. 2: 162-167, 172, 173; and Technical Reports Nos. 8, 9, 11) and by Eddinger (1970) have added considerably to our knowledge of the biology and evolution of the Drepanididae, but none of these studies has involved an approach to the avifauna as an integral part of the community. The community approach should provide a means of assessing species distinctiveness, the nature of ecological separation and/or overlap (and, thus, competition) within the avian community and the influence of environmental parameters on habitat selection, species abundance, distribution and diversity.

As part of the present studies now being conducted in subproject D-1, Conant is studying the role of land passerines, both native and introduced, in the biotic community. Effort is being concentrated in the following categories.

1. The nature of habitat utilization by all avian species in the community. - This project includes studies of habitat use in both normal maintenance activities such as feeding, and in breeding activities, especially nesting. Observations are being made in the wide variety of habitat types included along IBP Transects 1 and 2 (Tech. Rpt. #2, Fig. 2 & 3). A system of habitat classification has been developed, and data are now being collected on how each species uses various habitat zones (tree trunks, blossoms, leaves, etc.) for feeding, singing, and other activities. As active nests are found, data will be tabulated on the structure of the habitat immediately surrounding each nest to determine whether each species chooses a structurally distinct habitat for nesting.

2. Gradient analysis of avian community structure in relation to plant community structure. - The objective of this study is to determine how the avian community changes in structure (i.e., species density, frequency and diversity) over environmental gradients, such as elevation or moisture, and whether these

changes may be significantly related to similar changes in plant communities over these same gradients. Data on climate and vegetation have already been collected by other investigators working on the IBP study sites. Thirteen census transects (each 1 mile or more in length) have been established throughout the major vegetation types along IBP Transects 1 and 2. The "Count x Detectability" method of censusing, as described by Emlen (1971), will be used, and, hopefully, may overcome some of the difficulties of bird censusing in Hawaii discussed by Berger (Technical Report #8). Monthly censuses are being conducted at the same time of day, and under fairly uniform weather conditions.

This study was not begun until September 1972, so that insufficient data are available for a report at this time. New observations on the distribution and behavior of species, however, are pertinent for reporting (see subproject D-1).

Consumer relations

We are primarily concerned with the roles of consumers (animals) interacting with the producer and decomposer components of the ecosystem and with each other. It has been postulated, based to a large extent on continental biome studies under the IBP, that consumers are relatively unimportant in energy processing within terrestrial ecosystems: the primary flow is from producers to (microbial) decomposers which make nutrients again available to producers. This situation would be accentuated in completely native Hawaiian ecosystems (not influenced by man or by animals introduced by man) lacking any herbivores of even moderately large size. However, it can be accepted at this time that consumers have significant roles affecting both the floral composition and the rates of energy exchange, so that a system would have a fundamentally different floral character and rate of cycling in the absence of consumers. Some of the more obvious and important roles are pollination, seed-dissemination, direct effects of feeding by herbivores, and the influence of soil and litter faunas on the activity of decomposers. In recognizing the community as an aggregation of interacting organisms, we can assume that all consumers have some effect on this system; e.g., predators and parasites affect populations of primary consumers in greater or lesser degrees.

The role of the consumer can also be stated as its function in the ecosystem and this leads to a basis for characterizing functional groups. The "broad ecological niche" as used above is equivalent to the "functional group" as defined by the Working Group on Ecosystem Theory (proposal no. 6, Denver, January 1973). The comparison of functional groups among systems has been given the support of the Program Directors as one of the major directions that may be taken in achieving interbiome syntheses. Comparisons with continental systems are a usual approach in studies of island ecosystems, because of the depauperate and derived biotas of islands. The functional group as a basis for comparison was first applied to islands, but using different terms such as "ecological equivalents."

Most of our subprojects are concerned with species groups (related by life form or taxonomy) whose ecological roles we are investigating (see Tech. Rpt. #2: 217). Once the ecological roles of such species groups are more clearly defined, we are able to identify the functional groups in the island ecosystems under study. To determine functional groups, one must first inventory species. Higher category

determinations are inapplicable in nearly all cases because of the major differences in roles even between closely related species. Most of the consumer studies in this program involve identification and quantification at the species level.

Study of biotic interactions on islands is directed towards consideration of evolutionary factors. This is not only necessary because of the nature of island life, but also is an important source of conceptual development with implications for continental systems. Island systems tend to be relatively dynamic for several reasons. Various factors, that need not be analyzed here, lead to faster evolutionary rates (for some groups), faster turnover in species composition (introductions, extinctions), greater fragility in response to perturbations, and more flexibility in niche occupation by recently introduced forms. Most hypotheses concerning ecosystems that we are examining can be stated at least in part in evolutionary terms.

The studies of consumer relations follow the outline of integrated study sites and timing given in the Introduction. In addition, it is important to conduct some further, at least qualitative, sampling of other sites for consumer organisms. For example, we would like to know if a higher percentage of non-endemic species of cryptozoa characterizes the main soil and litter substrates of all parts of the islands as it does in the present study areas on the east slope of Mauna Loa. Some studies of consumer organisms, such as those on the lava-tube fauna (C-9), obviously require a broad survey approach covering all of the islands.

Consumers and their interactions are being studied under various projects according to habitat (e.g., foliar arthropods (C-4), soil and litter fauna (C-9), lava tube fauna (C-9), Metrosideros-associated fauna (C-6), systematic group (drepanidid birds (D-1), small mammals (D-2), sciarid flies (C-2), cerambycid beetles (C-3)), or specific interactions (effect of pigs on replacement of native grasses by introduced species (B-2), native birds in pollination of Metrosideros (D-3), effect of an introduced psyllid on endemic Acacia spp.(C-5)). The habitat- and group-oriented studies generally include species inventories, quantification by numbers and, in some cases, biomass, and examination of spatial and temporal distributions.

The following discussion of some aspects of consumer relations in Hawaii exemplifies the conceptual development of the current work. Some of the concepts have been generally accepted for many years, but the present studies provide the first well documented examples; others are hypotheses that require further testing.

Evolution of island biotas in the absence of certain functional groups of consumers has resulted in a high level of susceptibility (fragility) to the effects of these groups. There were no large herbivores in Hawaii prior to the coming of Polynesian man and the major impact of herbivores began less than 200 years ago. The current studies establish both the level of impact and some of the specific effects of large herbivores on the native vegetation. Goats were shown to largely stifle koa regeneration in mountain parkland, and to determine the total pattern of vegetation type in some lowland areas (largely to the exclusion of endemic plants with replacement by exotics). Current studies suggest that pigs have a major restrictive influence on the regeneration of Acacia koa and Cibotium spp., the two dominant plant types in the Kilauea Forest Reserve; it may be that this

plant community would gradually retrogress in the presence of unchecked pig activity.

Rattus rattus, which occurs at intermediate as well as lower elevations, destroys some native plants by girdling, and the same species may be a significant factor in the reduction of native bird populations through predation on eggs and nestlings. Again, the native forest birds have evolved in the absence of arboreal predators and would not be expected to have developed nesting behavior or other mechanisms adopted for defense against them. Ants have been shown to have a dominant influence on foliar arthropod distributions even within continental tropical ecosystems. The Argentine ant (Iridomyrmex humilis) may still be in the process of increasing its distribution at higher altitudes; the effect of this and other introduced ants on the population structure and survival of endemic insects may be difficult to assess but is probably highly significant.

Recent introductions, particularly "aggressive generalists," tend to invade a wide range of habitats in the absence of functional groups normally present on continents. Rodents, particularly Rattus rattus and Mus musculus, are prime examples in Hawaii and are each found in habitats from which they would be displaced by several other rodent species on continents. To some extent, there undoubtedly is niche as well as habitat extension, and Mus, for example, may occupy essentially the same niche in grasslands as some continental Peromyscus species that feed principally on seeds. On the other hand, it cannot occupy the niche of Microtus species which feed on grasses and are physiologically (including behaviourally) adapted for a low nutrient diet.

Extension of habitat and niche in the absence of competition is the precursor of adaptive radiation typical of insular systems. One might predict that Mus would eventually evolve a grass-feeding form in Hawaii. The drepanidid birds are one of the most spectacular examples of such radiation, including, for example, the "wood-pecker" adaptation of the Akiapolaau (Hemignathus wilsoni). Among insects there are many surprising examples unique to Hawaii, such as damsel flies breeding in terrestrial environments and the recently discovered complex of carnivorous moth caterpillars.

Study of the soil and litter fauna at elevations above 3000 ft., with particular reference to the permanent cryptozoa (Acarina, Collembola, some Coleoptera, etc.) has revealed that although most species are recorded for the first time in Hawaii, the great majority are probably recent introductions. This is true at 8000 ft. as well as at lower elevations. At altitudes above 3000 feet, foliar arthropods are largely endemic, and at high altitudes they are almost exclusively so. The soil and litter mesofauna appears poorly adapted for dissemination over large areas of ocean by non-human agencies, but is readily transported in soil by man. Once established on an island, these forms would tend to be spread over wide areas through human activity. Possibly the introduced species have displaced an endemic soil fauna from the principal habitats. The introduced species represent the less highly specialized segments of their higher taxa. Soil is a relatively homogeneous medium, and there may be few characteristics of soil and litter environments that would confer a special competitive advantage on soil organisms that had evolved in that particular geographic area.

The apparent displacement of the soil fauna is in contrast to the largely endemic foliar fauna at higher altitudes. At low altitudes in Hawaii there are

few endemic arthropods, but here the native vegetation has been almost entirely replaced by exotic plants. Some introduced foliar arthropods have spread to higher altitudes and quite rapidly; for example, the recently introduced Acacia psyllid. This suggests that the maintenance of some endemic species is partly related to their adaptations to the native vegetation, and associated organisms, so that they have advantages in competing with introduced species.

The above examples tend to support one of the hypotheses suggested in the original Hawaii IBP proposal (under hypothesis 2(b): "... penetration of exotics may be more a function of the life form of the potential invader in relation to the native life forms present in a community than the species diversity of that community." This does not mean that stability is not related to diversity; however, stability must be considered relative to a particular type of perturbation, and in terms of biotic interactions, stability is also related to the types of unfilled niches, the characteristics of the native species, and the characteristics of potential invaders.

One of the most interesting developments in the Hawaii IBP relative to consumer relations is the discovery of a rich fauna of troglobionts in lava tubes. This has disproved a number of tenents formerly held by biospeleologists. Contrary to earlier belief, the relatively ephemeral lava tubes of tropical oceanic islands are suitable environments for the evolution of cave-adapted faunas. The simplified ecosystems permit complete analysis of the food web, and this has been done, provisionally, for one system. A somewhat different, but roughly parallel, set of troglobionts have evolved in Hawaii in comparison with continental forms, permitting further understanding of characteristics that preadapt organisms for this habitat. Hawaiian troglobionts apparently evolved from relatively generalized native epigean or soil forms. However, there is essentially no overlap between the true cave fauna and the nearby soil fauna. Avenues for dissemination of species between lava tubes have been postulated.

5. GENETIC VARIATION WITHIN ISLAND SPECIES IN RELATION TO ENVIRONMENT

5.1 - 5.5

H. L. Carson

5. GENETIC VARIATION WITHIN ISLAND SPECIES IN RELATION TO ENVIRONMENT

"Ecological genetics" is the term used by Ford (1971), Creed (1971) and others to specify a branch of science which deals with the fundamental attributes of the evolutionary process. Evolution is simply descent with genetic change. The ultimate origin of such permanent change in organisms is the process of gene and chromosome mutation. Without these intrinsic "raw materials", no evolution can occur. On the other hand, the "directive forces" of evolution, such as natural selection, operate extrinsically through the environment. Such forces play a key role in determining what genetic variability is retained and what is eliminated. The mode of origin of new species and of new adaptations, therefore, can only be studied at the population level (microevolution). Not only must genetic variability be assayed but we must also seek to understand the environmental factors which influence the fate of the variability as it is built into the genetic basis of adaptations and new species.

Unfortunately, relatively few organisms lend themselves to the variety of laboratory manipulations necessary for thorough genetic analyses of visible, physiological, chromosomal, and molecular genetic variants. This is probably the reason for emphasis on the use of certain organisms, especially Drosophila flies, Lepidoptera, land snails and certain selected annual plants. The results of this approach have been extensively reported and reviewed (e.g., Dobzhansky 1970; Ford 1971; Mayr 1970) and form the basis for modern theories of how the process of adaptive evolution operates.

The usefulness of insular species

Organisms from insular ecosystems played a major role in the thinking of Darwin and Wallace, who pioneered the microevolutionary approach in the last century. Nevertheless, very few studies using modern methods have made use of such organisms. Accordingly, approximately ten years ago, a large effort was begun in order to exploit the obvious advantages of the Drosophilidae of Hawaii in this regard. Progress in this work has recently been reviewed (Carson et al. 1970).

A number of the goals of the project on the evolutionary biology of Hawaiian Drosophila are similar to certain of the objectives of the ISLAND ECOSYSTEMS IRP. Insofar as possible, an attempt has been made to coordinate the work of the two projects.

Organisms which are integrated into a mature ecosystem frequently show clear adaptations to the organic or inorganic environment or both. When one examines the species of such an ecosystem it is frequently difficult to know how recently the genetic basis of the species integration into the ecosystem has evolved. From the dynamic evolutionary point of view, relationships which are in statu nascendi are the most important.

For this reason, the ecosystems under close scrutiny by the ISLAND ECOSYSTEMS IRP on Mauna Loa on the island of Hawaii may be especially significant. The

entire island, and especially Mauna Loa, is geologically new; it therefore follows that the ecosystems found there may also show some novel features. It is nevertheless possible that the genetic adjustments of the species in the Mauna Loa ecosystems were actually accomplished millions of years previously on one of the northwestern Hawaiian Islands and, after transport to the island of Hawaii, little significant change has occurred.

That the ecosystems on Hawaii have at least some newly-evolved elements, however, is strongly indicated by some of the work on the large picture-winged Hawaiian Drosophila. The approximately 24 species of this group found on the island have been closely scrutinized by a battery of genetic tests. These tests confirm and strengthen the conclusions made on the basis of more conventional taxonomy. That conclusion is that all of them are species different from any found elsewhere in the world, including their close relatives on the adjacent Island of Maui. It would be hard to conceive of speciation occurring without being accompanied or immediately followed by at least some change in the mode of integration of the species into the ecosystem. How great these changes are is the subject of continuing investigation.

Speciating organisms: are they the dynamic elements in island ecosystems?

Drosophila, as was pointed out in the original Hawaiian IBP proposal, is an example of an extensively speciating group of organisms. By this very attribute, speciating organisms may help provide a clue as to what elements of adaptation in an ecosystem are likely to be either newly evolved or be in the process of evolving. Conversely, the non-speciating organisms in an ecosystem may represent those elements which are relatively stable. In the final summation of the work of the Hawaiian IBP, the enumeration of speciating and non-speciating organisms in various ecosystems should be examined to see what clues to the understanding of origin and stability of the ecosystem are provided.

Several other lines of evidence suggest that speciating organisms may represent a dynamic element within an ecosystem. Thus, data on the genetic and chromosomal variability in several species of Drosophila on Hawaii reveal that variability is extensive. This suggests that these species are indeed capable of change. In other words, natural selection in these species is potentially provided with ample genetic variability on which permanent changes in adaptive state might be built.

In the work being done directly under IBP auspices, two investigations are proceeding which attempt to relate genetic variability within certain species to environmental parameters within the ecosystem.

1. Microevolution within species. - Without trying to anticipate the outcome of experiments and observations which are in progress, the following account may be given. Kipukas Ki and Puaulu on the Mauna Loa Strip Road harbor a very unusual population of Sapindus saponaria. Two species of Drosophila endemic to the island of Hawaii (thus new in the geological sense) appear to be primarily associated with this tree. Drosophila mimica breeds on its fruits and Drosophila engyochracea breeds on the bark of fallen branches or broken trunks. Although abundant in these kipukas, both of these fly species and their host are exceedingly rare

elsewhere. The two kipukas referred to appear to provide a marginal environment for these large Drosophila, particularly because of the relatively xeric conditions prevailing in the areas where Sapindus grows. A number of species of Drosophila exist under xeric conditions elsewhere in the Hawaiian Islands but the species are few and their association is largely with trees other than Sapindus.

For the above reason, attempts are being made to determine the extent to which the genetic variability carried in these species relates to their ability to withstand dessication. The latter is judged to be a realistic natural stress factor which is at the same time reproducible with a test apparatus in the laboratory. These experiments involve observations of electrophoretically determined genetic variants in these two species from natural populations and the testing of various genotypic combinations in the laboratory. Both species appear to be newly-integrated elements in the ecosystem and may indeed be in an active process of adaptation at the present time. This work is being done by Mr. W. W. M. Steiner (E-1).

A further question can be raised. How stable over time are the genetic variability systems of organisms in an island ecosystem? A partial answer is being sought by Mr. Steiner. He is studying a number of polymorphic loci in D. mimica in a manner closely parallel to the study of Rockwood (1969), done in precisely the same area approximately five years previously. If a shift has occurred, this would suggest that active evolutionary changes have been recently occurring within the species.

2. The genetics of recent introductions. - One of the ecological realities of the current status of Hawaiian ecosystems is the extraordinarily large number of species recently introduced by man, either purposely or inadvertently. One may ask the question whether these species are successful by virtue of preadaptation or whether new basic genetic changes are occurring in their populations in response to their new role in the island ecosystems.

To attempt to answer these questions, studies of the population genetics of non-endemic species of Drosophila along the Mauna Loa strip road have been carried out. Drosophila immigrans, unlike most of the rest of the 22 drosophilines which have been recently introduced into Hawaii, appears to be a successful colonist in these high-altitude areas. Dr. Y. K. Paik and Mr. K. C. Sung have found the species up to the 7000 ft. level. Frequencies of chromosome inversions shift sharply between the 4000 ft. and 5100 ft. levels. Attempts are being made to interpret this difference according to certain environmental factors, and Mr. Sung is about to begin a series of laboratory tests with population cages which may shed light on the nature of this difference. At the present time it appears to be due to a difference in the action of natural selection on two different gene pools of the same species in two parts of the Mauna Loa transect.

Technical reports of IBP work have appeared or are about to appear which deal with introduced organisms such as the pig, the goat, the roof rat and psyllid insects (e.g. Psylla uncatoides). Paik's work on D. immigrans suggests that selection can alter the gene pool of an introduced species and produce new adoptive responses. On the other hand there is no evidence, so far, that changes of a speciating type are occurring. What he is finding in D. immigrans may well apply to the majority of introduced organisms which retain an outcrossed bisexual nature and which invade by building up large, freely-interbreeding populations in

island ecosystems.

The suggestion that newly-introduced populations may become genetically different from their progenitors must remain tentative until more precise data have been gathered. Mr. W. W. M. Steiner, however, has examined populations of a second introduced Drosophila species, D. simulans. Populations of this species on the Mauna Loa Strip Road show a large amount of electrophoretic variation. This seems to be greater than amounts recorded in the literature for this species from the midwest of the United States, for example.

3. Genetic changes in populations of endemics from Kilauea Forest. - Is there genetic variability within Drosophila species which are associated with a montane rain forest such as Kilauea Forest? Studies of D. silvestris, a species not found on the strip road, show that collections from within the forest, along transect 1, are highly polymorphic both for inversions and for electrophoretic variants. There is some possibility that a shift in frequency of several inversions, not accompanied by a shift in electrophoretic loci occurred between September of 1971 and May of 1972. Further studies of this phenomenon are in progress but the shift appears to be a slight one, if it is real. Nevertheless, the large samples analyzed from Kilauea Forest show that extensive variability can be a characteristic of populations integrated into what appears to be a relatively stable island ecosystem. This work is being done by Drs. E. M. Craddock and W. E. Johnson.

Non-speciating organisms: are they relatively stable elements in island ecosystems?

Parallel studies of Metrosideros collina as an example of a non-speciating organism have run into some technical difficulties. The method of choice for assaying the presence of genetic variability, electrophoresis, has not worked on this species, apparently because of some biochemical binding of isozymes. Although M. collina shows enormous morphological variation along the Mauna Loa Transect and elsewhere in the islands, whether this reflects underlying genetic difference or not has not been satisfactorily proven. Although seedling studies suggest that some of the differences have a genetic component, definitive proof appears to depend upon the outcome of layering and cloning experiments on this tree and Carolyn Corn is now planning to emphasize this approach.(B-6).

As a possible substitute non-speciating organism, attempts are being made to study electrophoretic variability in Acacia koa (W. W. M. Steiner). It is felt that this will not only help answer the question of how much genetic variability this species carries but will also permit a diagnosis of clones. Thus, along the strip road single massive koas are frequently surrounded by a growth of smaller trees. The latter are clonal derivatives of the central trees rather than volunteering seedlings. Proof of whether different individuals are involved in clonal formation could be achieved through electrophoretic methods if there were significant genetic variability present in this species. The members of a clone should be genetically identical and simple genetic tests should be able to establish this point. Koa, furthermore, grows both along the strip road under xeric conditions and in the deep montane rain forest, as at Kilauea Forest Reserve. Is the integration of koa into these two different ecosystems accompanied by significant

genetic difference? If it is, tests of the possible physiological basis of such differences might provide a basis for further relating speciating and non-speciating organisms to the dynamic features of the Hawaiian ecosystems.

6. PROGRESS OF SUBPROJECTS

6.1 - 6.59

Vegetation-environment correlation studies

D. Mueller-Dombois

(a) Vegetation map of Hawaii Volcanoes National Park

A vegetation map has been prepared for publication. The map was originally presented at the scale of 1:12,000 on two sets of each 53 sheets of (27 x 27 inch) aerial photographs. The two sets were presented to the Park Service together with the "Atlas for Bioecology Studies in Hawaii Volcanoes National Park" (Doty and Mueller-Dombois 1966:391). The map has been transferred from the air photos to topographic base maps at the scale of 1:24,000 resulting in 25 sheets with an index map. A few minor generalizations had to be introduced for this reduction in scale. The india-ink originals of this 1:24,000 map can be reduced to a scale of approximately 1:50,000 without loss of clarity. Publication of this map will cost approximately $1000. It serves and has served in part as the framework for the IBP studies in the National Park, for associated biological studies and for park management considerations.

Mueller-Dombois
Spatz

(b) Mauna Loa Transect Study: Gradient analysis of vascular plant communities

This study was described in some detail in Technical Report No. 2:31-41. Vegetation sampling was completed with an addition of three more relevés. The data were transferred to the computer and several initial synthesis tables were prepared including a table that shows species ordered into groups with defined distribution ranges. This ordered computer-printed table was distributed and discussed with all program participants that supply data for the integrated spatial distribution analysis. The table is used as a model for assembling the data of the other biota groups sampled along the same transect.

While the vegetation was sampled at 103 locations, a similar sampling intensity proved impossible for the other biologists working along the Mauna Loa Transect. A compromise was struck, and 14 focal IBP sampling sites were designated during a group field meeting in August 1972. The sites were those where most people had already sampled. Composite vegetation samples in form of relevé clusters at and around the 14 sites were selected and put on the computer for an overall correlation analysis which is expected to be completed in 1973-74. Integrated spatial sampling along another significant ecological gradient for comparison is anticipated for FY75.

Mueller-Dombois
Spatz

(c) Study on the influence of introduced large herbivores on the vegetation in Hawaii Volcanoes Park

A study of the effect of goats on the reproduction of Acacia koa trees was completed in form of Technical Report No. 3, and a manuscript was submitted for publication.

A second goat impact study on the lowland grass vegetation in the Park was completed as Technical Report No. 13. The manuscript will be submitted for publication shortly.

An experiment on competition involving Canavalia kauensis (a newly discovered endemic legume vine) and Melinis minutiflora (an exotic thick-mat forming perennial grass) is planned as a continuation of the lowland goat impact study. Results of this study will enable us to make predictions on the outcome of the goat-fencing program now planned for the Park lowland.

A third study dealing with a comparative analysis of grassland productivity under the present cattle grazing regime (outside the Park) and koa tree production on the same habitat was completed in the field. The habitat is that of the montane tropical rain forest at Kilauea Forest Reserve (from 4000 - 5400 feet elevation on the Mauna Loa east-flank). This study will form the habilitation-dissertation of Dr. GÜnter Spatz. He was supported as a Postdoctoral Fellow on the ISLAND ECOSYSTEMS IRP from April 1, 1971 through December 31, 1972. Part of his support was obtained from the BISHOP ESTATE (vehicle, fencing equipment, etc.), a local land-owning company. This support is gratefully acknowledged. Dr. Spatz left end-November 1972 for his home institute in Weihenstephan near Munich. Publication of his habilitation-dissertation is expected before the termination date of IBP by summer 1974.

(d) Vegetation-environment correlation studies on Oahu

Three studies were completed on the island of Oahu.

The first study dealt with a comparative analysis of the water relations of an introduced grass, Andropogon virginicus, and evergreen trees occupying the same lowland rain forest habitat on windward Oahu. The study was supported through this subprogram and resulted in Technical Report No. 4. The same material was presented by D. Mueller-Dombois at the Sino-American Forest Science Seminar on Forest Ecology and Genetics in Taiwan in April 1972. The manuscript has since been submitted for publication.

A second study originated from a request to the ISLAND ECOSYSTEMS IRP to supply scientific data and evaluation for an environmental impact statement relating to the influence of SO_2 fuming of the Kahe Electric Power Plant on SE Oahu. This investigation resulted in Technical Report No. 14 (by Mueller-Dombois and Spatz).

A third study dealt with a reanalysis after 20 years of seven plots in native dry-forest vegetation on NW Oahu. The study was initiated under NSF grant GB-4688 (under the direction of D. Mueller-Dombois). The core of the study was supported by a grant from McIntire-Stennis Forestry Research Program (F-674) to the Hawaii Agricultural Experiment Station. Additional facilities were provided by the ISLAND ECOSYSTEMS IRP. The study was completed as a M.S. thesis by N. Wirawan, and is listed under THESES with an Abstract. It will soon be prepared as a Technical Report and for publication in ECOLOGY.

N. Wirawan is now embarking on a Ph. D. dissertation program that was

developed as an outcome of the first mentioned study on the comparative water relations of an introduced grass and of evergreen trees forming separate communities in the rain forest climate on Oahu. His program will deal with the "Effect of vegetation cover on the soil-water relations in a tropical rain forest area." This program is under the direction of D. Mueller-Dombois and is within the objectives of the ISLAND ECOSYSTEMS IRP.

6.4

B-2

Studies of plant to plant interactions: studies of distributional dynamics

D. Mueller-Dombois

Two studies were initiated on the IBP Kilauea rain forest site as students' theses programs under this subproject in September 1971. These relate to a "Tree population structure and dynamics" analysis by R. G. Cooray and to a "Spatial pattern analysis of plant synusiae" by Jean Craine. The basic methodology of these studies was described in Technical Report No. 1:56-77. The progress in 1971 was reported in Technical Report No. 2:50-60. Since then both students completed their field work and both are currently engaged in the final writing of their M.S. theses, which are expected to be completed during the spring semester of 1973.

One of the students, R. G. Cooray, will thereafter continue with a Ph. D. dissertation program dealing with "The impact of feral pigs on the Hawaiian rain forest." Plans for the need of such a study were developed when it became apparent that the stocking density, distribution and presence of Acacia koa, forming the emergent trees in this rain forest community, are probably controlled primarily by the pigs.

A new Ph. D. program concerned with the "Competitive capacity of Hawaiian tree ferns" was initiated under this subproject in 1972. The need for this study arose from POSITION PAPER No. 3 published in Technical Report No. 2:205. The student, R. E. Becker, is currently supported by subproject B-5. The resulting dissertation will be a joint-effort between B-2 and B-5.

The planned competition experiment of Canavalia kauensis and Melinis minutiflora, which was an outcome of the goat impact study on the lowland vegetation, will become part of subproject B-2.

A study dealing with grassland succession as caused by feral pigs in the mountain parkland and savanna ecosystems on Mauna Loa has been completed and will soon be distributed as Technical Report No. 15 (by Spatz and Mueller-Dombois).

A continuation of this study is planned by fencing pig-scarified plots against further disturbance. The objective is to observe whether endemic herbaceous species will regain quantitative importance when pigs are excluded.

A study of primary succession on lava flows and ash deposits was completed with funds from this subproject. It resulted in Technical Report No. 10 (by Smathers and Mueller-Dombois).

B-3

C.H. Lamoureux
J.R. Porter
L. Matsunami

Progress report of phenological and growth studies, 1972

Phenological records are now being kept for over 50 spp. of perennial plants in the Mauna Loa Transect (including the Thurston Lava Tube plot), as well as other areas of the Park and in the Kilauea Forest Reserve.

With a few exceptions, all native plants and most exotics have annual phenophases; in other words, they have one flowering, fruiting, and vegetative flushing peak each year. However, each of these phases is often prolonged and would offer nectar and pollen, ripe fruits and seeds, and young shoots to primary consumers over several months' time each year.

The patterns of growth of species in the equable climate of Hawaii are not as distinct as those in more seasonal climates of the mainland. Detailed records of the times of the phenophases of 13 native tree species have shown a variety of patterns. Metrosideros collina has spring and summer flowering, as does Myrsine lessertiana, Coprosma ochracea, and Diospyros ferrea. The following flower in summer and fall: Myoporum sandwicense, Erythrina sandwicensis, Sapindus saponaria, and Cheirodendron trigynum. The others start flowering in late summer and continue through winter: Dodonaea viscosa, Santalum ellipticum, Ilex anomala, Sophora chrysophylla, and Acacia koa. Fruit ripening takes from 3 to 12 months depending on species. Most new leaves are produced from February to June within a month or two. Trunk growth has also been measured in these same species and is typically quite slow, a few millimeters in circumference each year. In Metrosideros, Sophora and Acacia, the times of phenophases differed at different sites. In the search for the causes of these observed differences, a technical report is being prepared relating the weather data and these patterns.

Comparing the patterns of 1972 with 1971, one finds relatively regular sequences of phenophases in each of the species (see Table 1). Observations will continue at all sites through 1973. If validation of three years' analyzed data is then needed, the number of sites should be expanded. We would also like to observe additional species.

Table 1. Examples of phenophases.

Species	"Peak months" 1971 Flowering	1971 Flushing	1972 Flowering	1972 Flushing
Acacia	Oct.-Feb.	May	Nov.-Feb.	May-Oct.
Cheirodendron	July	Feb.	June	Mar.
Coprosma	June	May	Mar.	May
Diospyros	May	Mar.	May	Jan.
Dodonaea	-	-	Sept.	June
Erythrina	Aug.	Nov.	Aug.	Nov.
Ilex	July	May	Aug.	May
Metrosideros	Apr.-June	Aug.-Dec.	Apr.-June	Aug.-Dec.
Myoporum	-	-	Aug.	July
Myrsine	May	June	Feb.	Apr.
Santalum	-	-	July	July
Sapindus	Aug.	May	Oct.	May
Sophora	Nov.-Dec.	July-Oct.	Oct.-Feb.	Feb.-May

B-4

Life history studies of important plants: Angiosperms

D. Mueller-Dombois
G. Spatz

Progress details on three investigations under this subproject were given in Technical Report No. 2:72-85.

(a) Koa growth rates in relation to age. - Monthly measurements over a one-year cycle have resulted in a technical report which awaits further editing.

However, the study needs to be continued to yield further data on year-to-year variation of diameter growth of koa and a larger population sample in certain size classes. Thus, continuation of this study is planned for FY 74 and 75.

A second report also awaits editing. It deals with koa growth along an environmental gradient (the Mauna Loa Transect) and with seasonal variations in koa growth.

(b) Koa reproduction study. - This study was completed by G. Spatz and resulted in Technical Report No. 17 which awaits typing. An abstract is shown in this report.

(c) Frost resistence in ohia trees. - Further laboratory studies on Metrosideros tree seedlings from different elevations were completed by Carolyn Corn under the direction of D. Mueller-Dombois. More data will be needed for a technical report or publication.

Subproject B-4 was eliminated in the revised budget for FY 73, because of the funding restraints imposed on our overall program. The elimination was considered temporary and funds are newly requested to continue subproject B-4.

Progress report on fern study (*Cibotium* spp., the Hawaiian tree ferns) — D. J. C. Friend

A study has now been completed of the effect of light intensity and temperature during growth on the photosynthetic plasticity of sporophytes and gametophytes of *Cibotium glaucum* collected from the Kilauea forest. Particular attention has been paid to a determination of the saturating light intensity and the light compensation point. A preliminary survey of results suggests that both the gametophytes and sporophytes show very limited physiological plasticity in regard to photosynthesis. Saturating light intensities were close to 1,000 ft-c and compensation points close to 30 ft-c for plants grown in deep shade or full sun. This lack of physiological plasticity would influence the ability of tree ferns to compete with other vegetation under high light conditions.

Gametophytes

Cultures were grown on agar at light intensities ranging from 2 to 4,000 ft-c, at daylengths of 12 and 24 hours and temperatures of 20 and 25°C. The growth of prothalli was measured by prothallial diameter, and in some cases, by dry weight. The effect of light intensity on the rate of photosynthesis was measured using an infrared gas analyser, and rates of CO_2 uptake were expressed on a fresh or dry weight basis, or on the basis of the chlorophyll content.

Gametophytes can grow even at a light intensity as low as 2 ft-c but only as filaments of cells. The typical cordate prothallus is formed at intensities of 10 ft-c or above. Gametophytes did not grow at intensities much higher than 1,000 ft-c even though they were kept in a saturated atmosphere. Bleaching of chlorophyll pigments occurred at the higher light intensities.

Sporophytes

The rates of emergence of leaves were measured over a period of one year on plants which were transplanted from the Kilauea site and grown at a series of light intensities from full sun to deep shade in a greenhouse under mist spray. The leaf area was greatest at low light intensities, and the chlorophyll content per unit fresh weight was greater than at high light intensities. The rate of photosynthesis was measured at different light intensities to obtain the saturating light intensity and the light compensation point. As mentioned in the introduction, these physiological characteristics showed little variation. During 1973, a new set of plants will be moved to controlled environment chambers at both 20 and 25°C and maintained at a series of low light intensities. Rates of leaf emergence will be followed, and in 1975, when the plants are fully adapted to their new light environment, photosynthesis measurements will be taken as before. This series will extend the previous results from the greenhouse series in an attempt to discover the lower light limit for the growth of the sporophyte.

Comparisons with other species

The lowest light intensity limit for seedling establishment of *Metrosideros*, an important constituent of the Kilauea forest, was determined by growing seedlings at a series of light intensities at 20 and 25°C in controlled climate chambers. The lower limit for seedling survival is close to that for tree ferns, about 10 ft-c. Growth rates of seedlings were followed by height and dry weight measurements.

A technical report and publication will shortly be written from the results outlined here.

B-2
B-5

Progress report on the competitive capacity of Hawaiian tree ferns

R. E. Becker

The Hawaiian tree ferns(Cibotium spp.) are a major component of the Kilauea rain forest and this study is being done under subproject B-2, and in conjunction with Dr. Friend's work under subproject B-5. Progress to date relates to obtaining background information on the taxonomy and geographical and ecological ranges of the species and to the initiation of detailed field studies.

In 1972 all of the herbarium specimens of Cibotium spp. at the Bishop Museum and the University of Hawaii were examined. The collectors' data were used to construct range maps for the six species on the six major Hawaiian Islands.

Library research was concentrated on obtaining copies of the original published descriptions of the species. This information was used to determine their correct nomenclature and to construct an identification key based on easily distinguishable morphological features.

In August 1972, field work was done in the IBP study site of the Kilauea forest and in the tree fern harvesting area of the forest. This work was mainly concerned with the establishment of two plots. The data from these plots, together with that from other plots to be established in the near future, will be used to analyze the population structure of the tree ferns in the rain forest. This work will form a portion of a proposed dissertation entitled: "The Competitive Capacity of Hawaiian Tree Ferns."

Preliminary results indicate that pig activity within the forest greatly influences the density of the tree fern stands. The results also indicate that vegetative reproduction is of major importance in the regeneration of the tree fern stands. Pig activity, or in the absence of pig activity, litter accumulation are two factors that seem to limit the effectiveness of sexual reproduction by a gametophytic generation.

B-6

C. H. Lamoureux
C. A. Corn

Progress report on genecological studies of Metrosideros

Technical Report No. 6, Seed Dispersal Methods in Hawaiian Metrosideros, has been published as a chapter in the 25th anniversary volume of the AIBS entitled Challenging Biological Problems: Directions toward their Solution, edited by J. A. Behnke. Technical Report No. 18, Altitudinal Ecotypes in Hawaiian Metrosideros, is being typed and soon will be submitted for publication. This latter report includes plants found along the Mauna Loa and Mauna Kea Transects. Continued IBP support on this project will lead toward a Ph.D. thesis expected to be submitted in August 1976, on Variation of Hawaiian Metrosideros.

Future technical reports currently planned will cover Metrosideros chromosome number, mechanisms of pollination, controlled field crosses, and germination of the F_1 offspring. Since this genus is the dominant tree along most of the Mauna Loa Transect and shares its dominance with Acacia koa in the Kilauea Forest Reserve, our work directly ties in with the studies of Metrosideros-associated insects (C-6) and birds (D-3). The mechanisms that govern Metrosideros growth, development, and evolution, are associated with fluctuations in population size of birds and insects living in close association with the plant.

Methods to propagate Metrosideros by clones are being refined. One of two problems that were hindering successful rooting of air-layered material appears to be solved, with the second problem close to solution. Once these barriers are removed, multiple cloning of select varieties can be tested in transplant stations at several altitudinal sites. This break-through can also lead to laboratory investigations of varietal tolerance to extreme conditions, such as temperature, humidity, wind and soils, and the mechanisms causing their success or failure in a particular habitat.

B-7

M.S. Doty
L.-L. McGurk

Progress report on the ecological role of soil algae

Tabulations of raw data have been made and, beginning September 1972, submitted for incorporation in the subprogram's data bank. As recoverable by taxonomy, by elevation, by site, or by time, different hypothetical relationships can be statistically tested. The usual time consuming "fierce" taxonomic problems of micro-organisms have been an especially accentuated barrier. However, the algal work is moving satisfactorily.

Climate, edaphic and vegetational variations with altitude were the first parameters around which sampling centered in the Hawaiian study area. Much of the effort in this phase of the work has been in technique development. The goal, keeping in mind relating the results to solar energy input and climatic factors, was to obtain quantitative appraisals of each species in terms of numbers of individuals per unit area. At least this much of the work should appear in a late 1973 or early 1974 master's thesis. It is anticipated that converting numbers of individuals to feed value (and other more meaningful values) will be a relatively easy future job (FY 74 or 75).

Correlation of algal populations with other organisms is being sought. Quantifying the algae in the samples used also by the terrestrial arthropod group under Dr. F. J. Radovsky and the fungi group under Dr. G. E. Baker is the approach. From hypothetical relationships supported statistically we hope to go to experimentation when there are close correlations. This can be done first by feeding the arthropods (especially in their larval stages) with algae so they can select their preference.

Seasonal variation studies are just now being initiated. The status of our earlier taxonomy and techniques prevented beginning sooner. We hope to continue this aspect of the work another year. For this purpose the number of sample sites will be reduced and the frequency of sampling increased to once per month. Since the few selected sites are among those already being sampled, sampling should be satisfactorily completed by March 1974. Analysis during the period before June 1974, should be relatively simple.

It is hoped a study of phyllosphere algae can be initiated and completed in FY 74. This would be correlated with the environmental factors listed above and with other organisms, especially insects and fungi. Experimental studies of the relationships between the algae and the larval insects that may consume them (with e.g., Delfinado), first qualitatively and later quantitatively, are planned. This ultimately quantitative work will endeavor to quantify the links between the algal and insect populations and their productivities.

Currently, an illustrated manual on the soil and litter algae is being prepared as a technical report and for use as a taxonomic guide. It is an extension of an initial effort, the master's thesis of Nelda Karganilla, done in cooperation with Dr. Malcolm Brown of the University of North Carolina. Dr. Brown is cooperating with further similar work on the soil and aerial algae of Hawaii to appear in a doctoral dissertation by Mr. Johnny Carson. Perhaps the first formal publication will consider the endemism and evolutionary adaptation of the algae in this particular volcanic area. For this purpose collections from similar locations

around the World have been processed, and outside funding has been obtained and applied to this aspect of the work as well as to some of the others.

Succession studies completed earlier (Doty 1967a, 1967b) are planned for extension and quantification to the mature tree-stage vegetations. The populations by FY 75 will have been described and quantified if the proposed budgets are approved. The goal is understanding the changing role of the algae and testing the stability of the algal communities at different successional stages.

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G. E. Baker
P. D. Dunn
J. Meeker

Progress report on the roles of fungi in Island Ecosystems

Non-parasitic fungi are associated with plants in a variety of ways. The relationship may be a close one to the point of reflecting endemism or it may be one contributing to the support of plants through decomposition and recycling of nutrients through the soil. Fungal communities active in this total spectrum begin with those of the phylloplane and progress through the litter zone to the soil. The B-8 subproject, which began with a study of the phylloplane mycota as a means of measuring coevolution in the fungi associated with endemic plants, has been expanded to assessing the roles of fungi in the litter and soil zones of these same endemic leaf and plant substrata.

The phylloplane fungi. - Studies of phylloplane mycota associated with three vascular plants endemic to Hawaii -- Metrosideros collina (Forst.) Gray var. polymorpha (Gaud.) Rock (ohia); Acacia koa Gray (koa); and Cheirodendron trigynum (olapa) -- extended from the fall of 1970 to August 1, 1972. Sampling sites included seven locations on the established IBP transect, Mauna Loa, Hawaii Volcanoes National Park, Hawaii, with elevations from 2,250 ft. to 8,500 ft.; a station in the Bird Park at 4,300 ft. where Cheirodendron is best developed; and Kilauea Forest, el. 5,290 ft. Samples of Metrosideros and Acacia were taken also from trees growing at approximately 600 ft. in upper Manoa Valley, Oahu.

Fungi were studied by several methods of recovery, viz. - 1) direct observation of leaves incubated in moist chambers; 2) plating out leaf washings and macerated leaves; and 3) swabbing leaf surfaces. The last method was employed only for Cheirodendron in initial studies. Other methods proved superior and thereafter were used routinely. Three selective media were chosen for plating. Plates of the same media were exposed to the air at the time of sampling at all elevations to determine the occurrence of fungi as airspora.

Studies of the structure of the three phylloplane substrata were made by examination of sections of living leaves and microchemical staining of such sections at the light microscope level. EM scanning studies of the surfaces of Metrosideros and Acacia were prepared by Dr. William A. Sakai, Department of Agronomy, University of Hawaii. A similar analysis by EM scanning will be made for Cheirodendron.

These approaches have yielded a variety of data which have been subjected to appropriate types of analysis. From the isolation methods a picture of the mycota as distributed among the three phylloplane substrata was derived. The total number of species recovered and identified was 168. Their distribution on these substrata was analyzed for numbers per leaf type, numbers on two leaves in all combinations (Metrosideros + Acacia; Metrosideros + Cheirodendron; Acacia + Cheirodendron), and those common to all three leaves. The distribution by elevation was also determined both with and without washings. The fungi represented only from air samples were noted. Table 1 summarizes these findings.

Similarities of constituent members of each leaf community were subjected to analysis by Sorensen's methods (SQ) and to computer analysis. Qualitative analysis of individual taxa was significant for those fungi with unique occurrence. Frequencies of isolation were noted for each taxon.

From such analyses, several trends appear. Metrosideros has a decidely

TABLE 1. Occurrence of fungi on leaf surfaces of three endemic vascular plants* in Hawaii and the air at the sample sites.

	Total number	Only on M	Only on A	Only on C	On M + A	On M + C	On A + C	On M+A+C	Air only	Adjusted total-air
Phycomycetes	4	2		1					1	3
Ascomycotina	9	3	2	1	1	1	1			9
Basidiomycotina	4	3	1							4
Fungi Imperfecti	151	62	18	7	19	11	2	16	16	134
Sphaeropsidales	20	9	2	1	3	1		4		20
Melanconiales	10	4			2	2		2		10
Moniliales	121	49	16	6	14	7	2	10	16	104
Moniliaceae	53	24	5	4	5	4		6	5	48
Dematiaceae	54	21	8	2	6	3	2	4	9	43
Stilbaceae	0									
Tuberculariaceae	12	4	2		4	1			1	11
Mycelia Sterilia	2		1						1	1
Non-sporulating mycelium**								+		
Total number of species	168	69	21	9	20	12	3	16	18	150
Percentage with air isolates		41.0	12.5	5.3	11.9	7.1	N.S.***	9.5	10.1	
Percentage without air isolates		45.7	14.0	5.9	13.3	8.0	N.S.	10.6	11.3	

* M = Metrosideros; A = Acacia; C = Cheirodendron

** Both moniliaceous and dematiaceous non-sporulating types

*** Not significant

larger population of taxa comprising its community (69 members or 45% of the isolates) than Acacia with 21 members (14%). The Cheirodendron population is even smaller but the number is skewed through fewer samplings so cannot be regarded as significant. Approximately 14% are common to Metrosideros and Acacia communities. Only 10% occur on all three.

The Metrosideros community is richer not only in numbers but in kinds of fungi (Table 1). This is notably so for pycnidial and other species of Fungi Imperfecti. For Metrosideros and Acacia numbers of moniliaceous and dematiaceous species are in the same range for each but several times more for Metrosideros than Acacia. Only one fungus, Cladosporium cladosporioides, was recovered at all elevations on both Metrosideros and Acacia. Aureobasidium pullulans, well-known not only as a cosmopolitan fungus adapted to a wide range of conditions but as a consistent member of phylloplane communities on active leaves, was found at all elevations on the transect for Metrosideros, at four out of five elevations for Acacia, as well as in Kilauea Forest and Manoa Valley. Several pycnidial forms occurred on both leaves at several elevations of the transect plus Kilauea Forest and Manoa Valley. The fungus representing Capnodiaceae Morphological Form I, Stevens, was consistently present on Metrosideros along the transect, in Kilauea Forest and Manoa Valley. It was never related to Acacia koa.

Differences in anatomy among the three leaf substrata are striking. Acacia koa phyllodes present very smooth surfaces on both adaxial and abaxial sides. Metrosideros leaves are distinguished by a continuous layer of abaxial hairs, well developed and intertwined. Cheirodendron also presents smooth surfaces on both sides. There is no doubt that the hairy abaxial surface of Metrosideros is a superior spore trap. Hyphae among the hairs are common and seen by both light and electron microscopy.

The diversity of these studies and their results have put us now in a position to relate the mycota of the phylloplane to those of the litter zone and those of the soil for the habitats selected, and additional correlative sites approved by the IBP project.

The litter fungi. - The phylloplane data for Acacia koa particularly was indicative of fungi present in the leaves as non-sporulating members. These fungi were recovered only from macerated tissues. They could be active contributors to the first level of activity in the litter zone. Pycnidial fungi also showed internal leaf association. Acacia leaves are much more resistant to decomposition than Metrosideros and Cheirodendron. When incubated in moist chambers Acacia leaves are consistently well populated by pycnidial forms. Presumably such taxa are among the first decomposers active in the koa litter zone. If the litter organisms do not come from the leaves themselves, the importance of the soil mycota becomes obvious. Gradients of activity between the contributors from leaf and soil communities are probable. In order to determine the succession of active consumers a study of leaves just prior to leaf fall could be significant. If some leaves, e.g., Acacia, are more resistant to decay than others, an analysis of the leaves as inhibitors to fungi, actinomycetes and bacteria becomes important.

The litter studies begun in the fall of 1972 concentrated on Acacia koa and Metrosideros, as these two endemic trees are considered to be the most significant

producers of litter on the transect. Litter collections were made at 5,500 to 6,600 ft. on the Mauna Loa transect in October. The intervening time has been spent in insolating and identifying the taxa from the communities representing these samples. For each the total population is being considered first, based on recovery by standard plating and isolation methods. Selective media for indicator organisms are being used for each site also. From this dichotomous approach it is hoped that a selection of significant organisms can be made. This information can then be extrapolated to sampling over the 14 selected IBP sites using the isolation of the indicator taxa as a measure of correlation. Until data from more sampling of the litter zone is available, it is futile to look for generalizations.

The sites selected for the initial work were related to Acacia koa. An in-depth study was pursued at the major transect sites at 4,500 ft. to obtain as broad a picture as possible of the community members. Then indicator organisms are to be selected so that the range of sampling can be extended to include as many of the selected IBP sampling sites as feasible, using the distribution of the indicator organisms as a measure of correlation.

Future programs. - Dr. Baker has no plans to carry this program beyond May 21, 1973, when officially she retires from the University of Hawaii. This subproject will continue under the direction of Dr. Martin Stoner. Mr. J. A. Meeker, graduate assistant on B-8 subproject will continue the phylloplane work during June and July. A final report will be made then.

A technical report is in preparation and publications on the phylloplane are planned.

Progress report on the occurrence and ecological roles of soil fungi associated with *Acacia koa* on the Mauna Loa Transect

Martin F. Stoner
Gladys E. Baker
Darleen K. Stoner

This research was undertaken in July, 1972 to determine the identity and distribution of soil-borne fungi in the rhizosphere of *Acacia koa* (koa), and to investigate evident ecological roles of the mycoflora. Preliminary efforts were focused primarily on identity and distribution of fungi since knowledge in this area is prerequisite to a critical study of ecological roles. Specific attention was given to the dominant cellulolytic mycoflora. The soil-borne mycoflora was chosen for study in an effort to complement previous mycological studies (Baker and Dunn, 1971) by elucidating the fungal populations in one of three distinct but potentially interrelated habitats: phyllosphere, litter and soil.

Methods

Composite samples of soil from the A_1 horizon were collected at 4,000' (Kipuka Puaulu) and 6,600' on the Mauna Loa Transect in the rhizospheres of both koa and, for comparative purposes, *Metrosideros polymorpha* (ohia). Each soil was analyzed for moisture and total organic matter content and for pH.

The mycoflora of each composite sample was isolated by three methods: dilution-plating, the Warcup soil plate, and the soil-washing technique employing corn meal, potato-dextrose, diet-food and soil-extract agar media (Johnson and Curl, 1972; Stoner, 1973). Hemp seeds and dead *Drosophila* were incubated in dishes containing water and soil for the purpose of isolating Chytridiomycetes and Oomycetes. Dilution-plating together with a medium containing cellulose as the sole source of carbon was employed to isolate the dominant cellulolytic mycoflora in collected soils. Sodium caseinate agar was used for the enumeration of soil-borne bacteria and actinomycetes. Each apparently different fungus appearing on soil plates was isolated into pure culture for eventual identification. The number of colonies developing on dilution plates was interpreted as a measure of the relative incidence of species in each soil-borne population.

Results

Over 500 isolates were obtained by the cited methods. Some fungi were isolated repeatedly, so the total number of different species recovered was under 100. Approximately 50 different species were isolated routinely from the soil samples. The identification of some fungi, especially those isolated on the selective cellulose medium, is in progress.

The percentages of isolates belonging to different taxonomic classes are: 6%, Oomycetes; 12%, Zygomycetes (Mucorales); 79%, Fungi Imperfecti; 2%, Ascomycetes; and less than 1% (?), Basidiomycetes. About 50% of isolated Fungi Imperfecti are species of Penicillium.

The largest populations of fungi, based on colonies per gram of soil as measured by dilution plating, were found in the soils around koa at 4,000' and 6,600'. Soils from both elevations yielded a similar number of colonies. Fungal populations at 4,000' in soil around koa were almost twice as large as those around ohia at the same elevation. At 6,600', the koa-related fungal populations were five times as large as those around ohia. Populations of bacteria and actinomycetes were also higher in soil around koa than in ohia soil. Soils collected at 4,000' possessed in general not only a larger, overall population of fungi, but also a more diverse mycoflora.

Certain genera of fungi occurred with considerably greater frequency than others. The genus Gliocladium and, particularly, the species G. deliquescens were found in varying levels in all samples. With the exception of the ohia soil at 6,600', the genus Absidia and, particularly, A. spinosa also were widely distributed. The genus Penicillium was represented by several species in every soil sample; however, this genus was noticeably predominant among the soil fungi near koa and ohia at 6,600'. Trichoderma viride was common around koa and ohia at 4,000'; however, it was uncommon (koa) or absent (ohia) at 6,600'.

Cephalosporium acremonium, Gliocladium roseum, Humicola fuscoatra, Mortierella ramanniana, Penicillium humuli, P. nigricans, P. variabile, Pestalotia planimi, and Pythium spp. were present, although not necessarily common, in all soils at both elevations.

The genera Cylindrocarpon, Fusarium and Gliomastix apparently were isolated only from soil around koa. The first two genera contain potentially pathogenic species.

Although identification of selectively isolated cellulolytic fungi is not complete, the genera Chaetomium, Penicillium, Gliocladium and Trichoderma appear to be major constituents of the cellulolytic populations, depending on the soil studied. Penicillium and Gliocladium were recovered from all soils. Gliocladium deliquescens was very common. Chaetomium was detected only in ohia soil at 4,000' and 6,600'. Trichoderma viride was not detected in ohia soil at 6,600'.

A statistical determination of the similarity of populations in different soils will be made after identification work is completed.

Conclusions and Discussion

Soils from the A_1 horizon under koa at 4,000' and 6,600' possess larger fungal populations than comparable soil from around ohia at the same elevations. The size of populations around koa suggests that those soils have a more active mycoflora. More study is needed to fully explain the greater populations around koa. However, two characteristics of koa soils, namely higher total organic matter content and extensive root populations, are potential contributing factors that should be considered. The difference in per cent water content between soils at 6,600' (as collected; koa soil, 26%; ohia, 14%) is suggested as another contributing factor. The species of fungi involved and the nature of their propagules, particularly with respect to efficiency of counting techniques, must be considered in the formulation of any explanation. Further attention should be given to the relationship between tree cover and the water content of underlying soils, and to relationships between levels of root development and the resident mycoflora.

The composition of fungal populations in the studied soils appeared to be related only in part to the associated higher plant community. Apparently, the distribution of some fungi is governed by broader and more complex environmental factors relating to altitude, soil development, and other conditions. The selection of certain fungal taxa as foci for future studies on the environmental distribution of soil fungi should take into account whether proposed research will deal with(1) the distribution of fungi according to gross-altitudinal differences, without specific regard to higher-plant associates; (2) the occurrence of fungi with respect to certain higher plants; or (3) comparisons involving both altitudinal factors and the nature of higher plant communities, as would be the case in a study along the Mauna Loa Transect. If comparisons of populations are to be made among all 14 IBP sites along the Mauna Loa Transect, the fungal taxa selected for study should be sufficiently abundant to support valid statistical analysis, and should serve to indicate ecological correlations by displaying differences in abundance and/or distribution of representative species according to elevation and/or association with koa or ohia. As indicated by this research, genera such as Cylindrocarpon, Gliomastix, and Fusarium, because of their apparent tree-related distribution, may be most useful in comparisons of fungal populations from different koa soils, where a particular higher plant associate is of special concern. Other genera such as Penicillium, Gliocladium and Humicola have a wider distribution, and therefore, appear to be better suited to comparisons of fungal populations along the entire environmental gradient, where there is concern for both gross-altitudinal factors and the influence of higher plant communities. The Mucorales (Zygomycetes) as a whole should be useful also in this latter capacity. Results further suggest that a combined study on (1) distribution along the Mauna Loa Transect, and (2) occurrence of cellulose decomposers should employ such selected genera as Gliocladium, Penicillium, Trichoderma and, possibly,

Chaetomium. The selection of certain fungal taxa for study allows for the greater use of selective media and, consequently, a more direct and efficient analysis of fungal populations.

A technical report is in preparation.

Current and Proposed Research

The findings reported herein indicate and support the next phase of our research: a study on the occurrence and distribution of fungi along the entire Mauna Loa Transect, utilizing selected genera or other groups as discussed above, and with particular attention given to cellulose decomposers. Soil samples are to be taken from 14 specified IBP study sites used by the integrated research groups so that results will support the synthesis of information from different projects. Preliminary studies in this area have focused on the distribution of Penicillium spp. and genera of the Mucorales. Gliocladium spp., Trichoderma spp. and Chaetomium spp. also are considered for study.

Additional research will concentrate on the occurrence and distribution of fungal decomposers utilizing cellulose and lignin. These studies could be coupled with the above project.

Additional areas of research that deserve attention include the occurrence of mycorhizal and plant-pathogenic fungi along the transect, and the development of endemism in soil-borne fungi. The latter area could be developed together with research on decomposers, since enzymatic activity could be used as a measure of physiological endemism.

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C-1

Biosystematics of Hawaiian Diptera: Diptera fauna in native forest litter-distribution, abundance and factors responsible for variation.

M. D. Delfinado
D. E. Hardy

This report covers litter samples collected and processed from 9 IBP sites (see Mueller-Dombois Memo, Aug. 21, 1972) transect segments 12, 11, 10, 8, 7,7, 7, 6 & 5 and Kilauea forest plot 1 for comparison, December 1971 through August 1972. However, sampling during the first 3 months has been limited as to location of sampling sites. The method used here departs radically from the usual techniques of litter fauna collecting in that the substrates are brought to the laboratory and placed in gallon jars for emergence of adults. This method has been adapted from Heed (1968) and has been found satisfactory in censusing the diptera fauna in litter.

Preliminary findings: 1) identification of specimens to species level is underway and indicates a high percentage of endemicity; 2) distribution pattern appears to be influenced by vegetation component particularly because of the biochemical properties of the leaves, and plant species supplying litter may greatly influence the diptera population which feed on them; 3) season (climatic) and site (altitudinal) factors seem to affect considerably the fauna, hence the rate of litter breakdown varies.

We will continue this study for a full year and employ the emergence trap method for measuring population density in one sampling site, e.g.,Kipuka Ki. This additional test method, we hope, will give us further information on field population and community studies. A detailed report is planned for publication at the termination of the study.

Plan of work for year 1974-75 - The evolution of Hawaiian Telmatogeton (Chironomidae)

This study was started in 1971 on the endemic species of chironomid in an attempt to trace the origin and evolution of the freshwater Hawaiian Telmatogeton found breeding in Wailuku River, Mauna Kea Transect. Due to lack of funds, this study was stopped. From our preliminary investigations, this species indeed offers a unique opportunity for evolutionary study. Members of the genus Telmatogeton occupy marine habitats, but in the Hawaiian islands endemic species are confined to rapid mountain streams. Preliminary orcein smears made by Dr. Carson on the larvae revealed that these have extraordinarily large and favorable salivary gland chromosomes. The larvae can be readily obtained and it is possible to rear them in the laboratory. It is planned that Dr. Lester Newman, Portland State College, will be brought to Hawaii to study the chromosome variations and evolutionary development of the Hawaiian species from the marine habitat. Dr. Newman has had considerable experience in cytogenetics of freshwater Diptera and should be able to make very important contributions to our understanding of evolutionary processes.

Progress Report on the ecology of Hawaiian Sciaridae.

W.A. Steffan

One technical report, Ecological Studies of Ctenosciara hawaiiensis (Hardy), has been published and an expanded version of this study has been submitted to Pacific Insects for publication. Two additional technical reports are in progress and will probably be completed by April 1973. One is on the Sciaridae of Kilauea Forest Reserve and the other on the Sciaridae along the Mauna Loa Transect. The latter two reports tie in directly with two of the integrated subprograms of this project.

A paper on the complex systematics of Bradysia tritici (Coquillett) has been completed and will be submitted to the Proceedings of the Hawaiian Entomological Society in December 1972. Also a paper describing the new species of Sciaridae discovered in the Kilauea and Mauna Loa studies will be submitted for publication by April 1973.

Collections of Sciaridae from other subprojects, C-1, C-4, and C-9, have been identified and are being incorporated in the next two technical reports. Combined with the Malaise trap studies in Kilauea Forest Reserve and along the Mauna Loa Transect and supported by laboratory studies of life histories, these data will provide a fairly comprehensive picture of the ecology of some of the more common Hawaiian Sciaridae and their relationships to other components of the various ecosystems being studied.

Dr. Bridges and his student are working on a model of Ctenosciara hawaiiensis (Hardy) based on the data from Technical Report No. 7. Additional data were requested on the life history of this species and have been provided. The fecundity of this species needs to be studied for a more satisfactory model and these studies will be done during the early part of 1973.

C-3

J.L. Gressitt
C.J. Davis
G.A. Samuelson

Progress report on cerambycid-borer study

This study has been progressing in two directions: 1) The role of the cerambycids and other borers in the ecosystems under general study; 2) The evolution and host relationships of the cerambycids in the island chain as a whole. During 1972 the study was further augmented by addition of an investigation of the relationship of borers to the 'ohia decline' in Metrosideros, mainly in the Saddle Road area of the island of Hawaii, between the Mauna Loa and Mauna Kea transects. This added investigation is funded by a grant to the Bishop Museum from the U.S. Forest Service, and involves Gressitt, Samuelson and a field assistant (W. Ruffin), with Davis as advisor. J. Jacobi assists in the sampling work in the IBP transects.

Plagithmysines: The major group of cerambycid-beetle borers native to Hawaii, and the only group which has speciated, is the plagithmysine complex, now treated as a single genus, Plagithmysus (Gressitt 1972b), of over 130 species. These are primary borers of native woody plants. The hosts include a number of the genera forming major constituents of many of the Hawaiian ecosystems.[1] In general, the most common trees are preferred by the beetles, except as noted below, and rare trees may not be attacked. The beetles are highly host-specific and cases of a species of beetle attacking more than one genus of host are rare.

Of the common woody plants in the study areas, Acacia koa and Metrosideros collina (polymorpha) are more or less commonly attacked by these beetles with usually two species to each. Sophora usually also has two species, as may Dubautia. Other genera such as Pelea, Myoporum, Vaccinium, Geranium, Sapindus, Pipturus, Chenopodium, Fagara, Charpentiera, Bobea, Diospyros, Dodonaea and Rubus each have a species boring in them in some part of the island of Hawaii. Records from Myrsine, Pouteria, Platydesma, Santalum, Perottetia and Mezoneurum are extremely rare. On some islands Ilex, Pittosporum, Bidens, Argyroxiphium and Smilax have plagithmysine associations, but such feeding has not been detected in the study areas, and not on the island of Hawaii with two exceptions (Ilex and Smilax, Kohala Mountains). The common woody genera Cheirodendron, Tetraplasandra, Styphelia, Coprosma, Canthium, Wickstroemia, Osmanthus, and many less abundant genera[2] have no records of association of plagithmysines.

These beetles appear not to occur throughout the altitudinal ranges of their host trees. Their relative abundance in different areas sampled is not uniform and the factors involved are complex, including effects of man, of feral animals, disease, weather, other insects and other less obvious influences.

It has been suggested that the role of consumers has been neglected in terms of its importance in ecosystems and its effect on evolutionary selection of plants. The plagithmysines are feeders in wood, influencing the cambium to varying degrees. Since they probably relate in the main to unhealthy trees, their selective importance is difficult to determine. However, they

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[1] Technical Report No. 5.

[2] Technical Report No. 2, p. 123, but eliminate Myrsine from list.

certainly serve the function of starting the breakdown of surplus or dying fractions of trees, and dead trees. Whether they actively reduce photosynthesis in killing branches is uncertain. In some cases they must reduce growth rates and increase wind damage risk, where main stems and roots are heavily attacked (common with some species in Pelea and also the large Plagithmysus perkinsi in Myoporum). It has been suggested that the role of herbivores is to selectively eliminate those producers, or their photosynthetic parts, that are not utilizing or will not be able to utilize available solar energy to the maximum possible; thus, that the herbivores favor the development of healthy plants. The plagithmysines would seem to fit this hypothesis in part, since most of them bore in or close to living parts of the plants. At the same time, these beetles may also do serious damage to some trees. Perhaps even some of the latter effect may serve to eliminate "unhealthy" trees and thus perform a beneficially selective function.

During the year, further data have accumulated, in particular on the relationships and habits of Plag. varians in koa. It is now clear that both koa plagithmysines prefer illuminated areas, and fly above the forest understory. Also, that they prefer terminal branches (the smaller species is restricted to these). P. varians will avidly attack major trunks or branches when trees are injured, such as by branches falling or splitting as a result of wind and/or termite work, and particularly when such branches or trunks are exposed to sunlight. Planted young koa trees are also vulnerable to attack. A row at start of the Strip Road had most of upper branches heavily attacked if not killed. Dying back has been the result of both plagithmysine species attacking, and this has apparently been fostered by the lack of canopy shade. P. bilineatus in ohia proves to be much more abundant in the 'ohia decline' areas than along the Mauna Loa transect. The former are much more open in general. It is presumed that most flight is near the canopy and does not involve great distances. Planted trees away from normal populations are usually not infested. Of course, over geologic time, wind has distributed these species from one island or kipuka to another, but this has not been frequent enough to prevent reproductive isolation on different islands, at least.

Some of the above observations indicate that the beetles are favored and the hosts are further damaged when disturbance (whether from lumbering, road building, storm winds, or otherwise) exposes, trims, breaks or otherwise handicaps the trees. Thus the beetles tend to kill or help kill trees which have suffered disturbance.

Other borers: The two species of endemic cerambycid beetles which have not speciated belong to Parandra and Megopis - larger and more primitive types than the plagithmysines. In general they feed in dead wood and are polyphagous, although Parandra may feed in living, injured koa trees. Introduced species of Cerambycidae for the most part restrict themselves to introduced trees, and to a great extent attack dead wood. A few of them attack native trees in disturbed environments, particularly in drier areas.

Other beetle borers in the study areas include two species of Xyleborus, in the bark beetle family. These in general attack declining trees or tree parts, and many of the above observations on plagithmysines apply also to these beetles. They are much less abundant than bark beetles are in most

temperate forests. Other borers in the transects are usually secondary to the attacks of the above beetles. Most of them are concerned with the breakdown of dead wood, and may have little or no effect on the living portions of plants. This is true of many of the lepidopterous borers, which generally appear in old cerambycid borings. However, there are moth borers in living parts of Charpentiera, Myrsine, Cyrtandra and Broussasia, some of which are quite damaging. The termites to a great extent have little effect on growing parts, although sometimes living portions of trees are affected by breakage resulting from termite attack in dead portions. Other dead-wood inhabiting animals such as isopods, amphipods, cockroaches, cryptostigmatic mites and millipedes come in the later stages of breakdown, after the beetles, moths and termites.

Technical Reports: Gressitt, J.L. and C.J. Davis. Seasonal occurrence and host-lists of Hawaiian Cerambycidae. Techn. Rpt. No. 5, 1972.

Another technical report is in preparation, on the evolution of the Hawaiian plagithmysines.

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Progress report on phytophagous insects - sap & seed feeders (Heteroptera). W. Gagne

Spatial Organization of Foliar Insects on Two Community Structure Forming Plant Species Along an Altitudinal Gradient

The foliar arthropod community of mature ohia (Metrosideros collina) and koa (Acacia koa) has been sampled bimonthly from March 1971. Arthropods were removed by use of an insecticidal fogger with industrial pyrenone as detailed in Technical Report No. 2. There were 9 sampling stations from 50' to 7,000' elevation and recently a site at 8,000' was added.

Distribution of taxa

Heteroptera and Collembola were identified to species. Coleoptera, Diptera, Homoptera and Hymenoptera were taken to family level, while the remaining groups were classified to order, or subordinal level in Acarina. Collaborators are identifying several other groups to species level. About the same number of taxa were found on ohia and koa although many species were not shared.

On ohia the richest arthropod communities in terms of number of taxa occurred at mid elevations and were about three times that at sea level and at 8,000'. The number of taxa was uniform between 2,500' and 3,900'. About 16% of the taxa occurred at all elevations. They comprised the following groups: chalcidoids, microlepidoptera, spiders, bark lice, predaceous mites, drosophilids, lacewings, sciarids, thrips and the wholely exotic lady beetles, ceratopogonids and Entomobrya nivalis (Collembola). Most of the former groups appear to contain predominantly exotic species in the lower elevations, excepting the endemic Psyllidae (Homoptera). Conversely, 14% of taxa found only between 2,500' and 7,000' appear to contain mostly native taxa. Most of the endemic bug species also occur at 8,000'. At least 6% of the taxa occur only at mid elevations and the endemic Coleoptera account for most of these. The 5% of taxa found only near sea level appear to be all exotic. On koa, about 36% of the taxa occur throughout but this host occurs only between 4,000' and 6,600' on the gradient. About 15% of the taxa are each restricted to sites near 4,000' and in the Kilauea Forest Reserve (5,400'), respectively.

Fluctuations of certain Heteroptera

On ohia, 3 groups of endemic true bugs were selected for detailed analysis. These were the seed feeders, Oceanides vulcan and O. pteridicola, the sap feeder, Sarona adonias, and the insect predator, Nabis oscillans. Oceanides populations were highest during the spring months, between 2,500' and 5,400', and during December at 7,000'. Their populations were uniformly higher at mid elevations. S. adonias populations were higher in the lower elevations (2,500'-4,000') during the spring, and during the fall in the 5,400-7,000' range. N. oscillans occurred at trace levels at 2,500'; was absent on the Mauna Loa transect above 4,000' but was present in the Kilauea Forest Reserve (5,400'). No pattern of abundance was discernible for this species except that populations were highest in the rain forest at 3,900'.

Fluctuations of these species are hypothesized to correlate with certain host phenology events. The following factors are being investigated: correlation of the abundance of 1) seed feeders with the phenology of seed production, 2) sap feeders with flushing of terminals and 3) predators with the richness of the prey species in each community. Life history determinations are being made on other prevalent Heteroptera.

Biomass measurements

The standardized mean arthropod biomass on ohia was uniform between 3,800' and 7,000', lower at 2,500', and subject to great fluctuations at the two elevational extremes. Near sea level large roaches and their parasites raised the otherwise low biomass comprised mostly of ants. At 8,000' the intertree variation was great between samples in exposed to wind (low biomass) versus sheltered situations. Spiders and Hemiptera, both native, comprised most of the biomass here. On koa there was more uniformity in weights; spiders and caterpillars comprised most of the biomass. In terms of numbers of individuals, Psocoptera outranked others both on koa and ohia. Sporadically, there were large populations of Collembola.

Prevalence of ants

Ants are considered to have great impact on nonadapted insular arthropod communities. They were recovered between 50-7,000' and all samples between 50-2,500' contained them but the populations were 10-100 x those at higher elevations where they occurred at trace levels. Psyllidae were the most "tolerant" of the endemic groups to ants.

Foliar Insect Community Structure and Niche Differentiation in an Island Rain Forest

Sampling sites were established near the centers of the 4 surveyed transects in the 200 acre tract of the Kilauea Forest Reserve (5,400'), Island of Hawaii. Portions of mature koa were sampled by fogging with pyrethrum and the foliage of large limbs in the 30' to 70' interval above ground onto $5m^2$ funnels. Pole-sized ohia were likewise sampled by attaching the corners of $2.5m^2$ funnels to four adjacent trees. Samples have been taken bimonthly since March 1971.

Population periodicity

On ohia there were 2 arthropod population peaks per year, in August and February, while on koa there was one population peak during the winter months. The higher percentages then of immature hemimetabolous insects were taken to indicate a population build-up. With more sampling, intertree variation for pattern analysis will be attempted.

On both hosts the fluctuations in the saprophagous component, comprised mostly of Psocoptera, were greatest. The presence of epiphytic cryptogams and associated detrital material especially on ohia also influenced this component. This factor appears most difficult to quantify in order to define the more strictly ohia associated fauna. On koa, the presence of dead limbs

and twigs was a factor here. The phytophagous and entomophagous fluctuations are being statistically analyzed to elucidate patterns.

Composition of taxa

There were higher numbers of taxa on both hosts here than at comparable elevations on the Mauna Loa Transect. About 3% of the taxa on ohia and about 13% of the taxa on koa have been encountered only in this rain forest. The lady beetles, a wholely exotic, otherwise ubiquitous group have not yet been taken in samples here. About 18% of the koa samples contained ants, but at what could be trace levels when compared to lowland ohia samples. No ants have yet been taken on ohia. The percentage of known exotic taxa in samples here appear to be among the lowest on the transects, although considerably more analysis is proceeding along these lines.

Arthropod biomass

The mean biomass on ohia was higher than that from the same elevation on the Mauna Loa Transect. Weights of samples from koa on the Mauna Loa and Kilauea Forest Reserve Transects were grouped in the 0.6g to 0.75 gm range. Taxa contributing to the bulk of the biomass were spiders on both hosts, and Hemiptera on ohia, and geometrid larvae on koa. The soft bodied spiders and Lepidoptera larvae all appear to be cryptic in habits and coloration - a reflection of heavy bird predation?

Insect bionomics of koa seedlings

Other project investigators are demonstrating that practically all koa seedlings and suckers within reach of feral pigs are being destroyed. The sparing regeneration appears to be taking place almost entirely on the bases of wind thrown koa above the reach of these animals. A studywas recently initiated to determine the fate of such regeneration with respect to insect depredation. It was determined that most of these plants are being attacked by a complex of lepidopterous larvae (bagworms, cutworms, and terminal borers) as well as sap sucking delphacids and mites. Whether this assemblage contributes other than to crown distortion remains to be elucidated. The delphacids and mites are said to be a factor in seedling mortality in the Laupahoehoe Forest Reserve from a State initiated study some 50 miles north in a recently logged forest.

Progress report on effects of sap-sucking Homoptera on Hawaiian ecosystems.

C-5
J. W. Beardsley
John R. Leeper

Psylla uncatoides (Ferris and Klyver) is a recent accidental introduction into the Hawaiian Islands. It breeds on endemic Acacia species, A. koa and A. koaia, and is best adapted to areas of moderately cool climate where its population dynamics are tied closely to the flush phenology of the host trees. The mountain parkland and koa savannah regions of Mauna Loa above 4,000 ft. elevation and the Acacia koaia Reserve (Kohala Mts., 3200 ft.) appear to have optimum conditions for psyllid development. In these areas peak psyllid populations are followed by extensive dieback of flush growth. We believe that psyllid damage may be the reason why little flower set and no seed production has occurred at the A. koaia Reserve during the past two years.

Several kinds of predatory insects (coccinellid beetles, lacewings and syrphid fly larvae) which normally attack aphids have been found preying upon P. uncatoides on Hawaii. However, the species present are ineffective in controlling the psyllid populations. No parasitoid insects attack this psyllid in Hawaii. In Australia, where P. uncatoides is endemic, both insect predators and parasitoid wasps were found to attack this psyllid. Certain of these are now being cultured under insectary conditions in California where P. uncatoides also is a pest. In collaboration with the Hawaii State Department of Agriculture, we plan to introduce a few of these Australian psyllid enemies to Hawaii in an attempt to achieve biological control of P. uncatoides.

The control agents that we propose to introduce (which I located and studied while on sabbatical leave in Australia during 1971-72) are intimately associated with Psylla species on Acacia in southeastern Australia. These psyllids are generally maintained at low, non-damaging population levels in Australia and are often difficult to find there. Several species of psyllid-associated predators were discarded because they belonged to groups known to have fairly wide host preferences (e.g., lacewings and syrphid flies). The natural enemies we have selected for possible introduction include several species of parasitoid wasps of the family Encyrtidae (undescribed species of Psyllaephagus and related genera). These insects are highly host specific and although some were found to attack more than one species of Psylla on Acacia, none of these species were ever found associated with other genera of Psyllidae. There are no endemic psyllids on Hawaiian Acacia species, and the endemic psyllid fauna contains no species either closely related to or similar in habit to P. uncatoides. In fact, all the endemic Hawaiian psyllids belong to a different subfamily (Triozinae) than does P. uncatoides. Therefore, there appears to be no likelihood that these encyrtids will parasitize endemic psyllids.

The psyllid predators which we propose to introduce are two species of coccinellid beetles. These coccinellids are specialized psyllid predators which in Australia were found associated only with Acacia psyllids. They prey principally on the eggs and young nymphs, which are situated in exposed places on the phyllodes and young shoots. Australia has a well-developed psyllid fauna. Eucalyptus species, for example, are hosts for a large fauna of lerp-forming species, as well as forms with free-living nymphs. Although I spent

considerable time examining Eucalyptus while in Australia, I never found these coccinellids preying on Eucalyptus psyllids, even though the latter were sometimes plentiful. Since our endemic Psyllidae occur on other hosts and are mostly of different habits, with nymphal stages sparsely distributed and often enclosed within galls, it is extremely unlikely that these coccinellids will have any measurable effect on their population levels. One of the two species which we propose to introduce, Harmonia conformis, was actually liberated in Hawaii many years ago. It was introduced here from Australia in hopes that it might become an effective aphid predator, but it failed to become established, probably because there were then no Acacia psyllids for it to prey upon.

Another question which has been posed is whether these coccinellid predators would destroy endemic Homoptera on Acacia species which occupy niches similar to that of P. uncatoides. It is possible that some minor predation on native leafhoppers and planthoppers (Cicadellidae and Delphacidae) might occur, particularly after psyllid populations have been reduced. However, coccinellids are virtually never effective predators against leafhoppers and planthoppers. These insects are relatively large and active and our endemic species rarely occur in sufficiently concentrated colonies to produce a prey density sufficient to support coccinellid populations. About the only situation where coccinellids might become a significant mortality factor operating against native leafhoppers and planthoppers would be during rare outbreaks of these insects such as the recently reported outbreak of the koa planthopper, Nesosydne koae, on the Laupahoehoe Forest Reserve. In such cases predation by coccinellids would be considered beneficial.

Uromyces koae Arthur is an endemic rust specific to A. koa and is believed to be disseminated in spore form via the wind. In checking the integument of psyllids collected from non-rust terminals in a rust area, 63% were found to be carrying the spores. This is an indication that P. uncatoides may be acting as a mechanical vector of the rust.

The research completed to date has:

1. Shown that Psylla uncatoides can cause appreciable damage to Acacia koa and A. koaia in areas where climatic conditions are favorable for maximum psyllid population development.

2. Demonstrated the ineffectiveness of the existing natural enemies in controlling P. uncatoides.

3. Indicated the optimum time of year for introducing new natural enemies of P. uncatoides into Hawaii.

4. Provided population data by which we can later evaluate the effectiveness of introduced natural enemies in controlling P. uncatoides.

5. Provided those studying other aspects of the endemic Acacia spp. ecosystems data to better evaluate the impact of P. uncatoides on their studies.

A technical report is now being written on the first year and a half's research and will be published within the next year. The research is being conducted and a dissertation covering this work will be prepared in partial completion of Ph.D. requirements by John Leeper. Thesis research is expected to be completed in June, 1975.

C-6
T. Nishida
F. Haramoto
L. Nakahara

Progress report on faunal research on Metrosideros

Of the phytophagous arthropods, the psyllids appear to have the greatest influence on Metrosideros. For this reason, studies were undertaken to determine the relationship between this plant and the psyllids. The studies commencing on January 1972 were restricted to designated areas at elevations of 4000', 5500', 6600', 7000' and 8000'. Previous studies had shown a close relationship between galling and flushing, so the numbers of terminals with buds, flushes and unopened galls were recorded to observe the cyclic phenomena of the psyllids.

The sap-sucking pysllids feed on the leaves, petioles, buds and stems of a number of plants in Hawaii. Eleven endemic species of psyllids have been recorded on Metrosideros of which 4 have been from the island of Hawaii. Our studies have shown that at least 5 species of psyllids occur on that island and that 4 of them are present along the Mauna Loa Transect #1. Those present along the Mauna Loa Transect #1 are 3 species of Trioza which form enclosed galls on leaves, flowers and stems, and a species of Kuwayama, K. minuta, which forms pit or open galls on leaves of Metrosideros collina var. incana. Two out of the three species of Trioza are new species and referred to in this report as Trioza #1 and Trioza #2. Trioza #1 forms flat galls, Trioza #2 cone galls and Trioza hawaiiensis Crawford stem galls.

The close relationship between Metrosideros and the psyllids is evident in the egg laying behavior of the latter. Both Trioza #1 and Trioza #2 lay their eggs on branchlets that terminate with an enlarging bud or young flush. The eggs are deposited in various places on the petioles, stems and undersurface of leaves. The eggs of T. hawaiiensis, on the other hand, are deposited on the undersurface of leaves and on the stems of young or maturing flushes, while those of K. minuta are deposited on the uppersurface of the leaves of young flushes. The nymphs of Trioza #1 and Trioza #2 seek the underside of young leaves for feeding. The nymphs of T. hawaiiensis feed on the base of terminal and axillary buds and those of K. minuta feed on the surface of leaves where the eggs were deposited.

Metrosideros phenology has a great effect on psyllid populations. The data show that (1) psyllid abundance is directly related to the flushing cycle, and (2) the distribution of individual psyllid species along the transect and on the plant, the shape of galls characteristic of a particular species and the apparent coexistence of plant and insect is without great detriment to either. All this suggests a close evolutionary relationship between this plant and insect, and (3) tree-to-tree differences in psyllid galling suggests the polymorphic nature of Metrosideros even within a particular variety.

Psyllid galling is closely related to Metrosideros phenology (Figs. 1 and 2). Flat galling indices obtained from 4000' are utilized to emphasize the relationship of the leaf gall formers with the plant's flushing. Peak flushing and a corresponding peak in flat galling are highest during the winter months when temperatures are lower and rainfall is more abundant. The situation seems favorable for the flat gall psyllid since the adults would then reach a peak during the drier and warmer spring and summer months. This close cyclic relationship between plant and insect is seen along the entire transect, although it is more dramatic in areas where the overall abundance of the psyllid is greater.

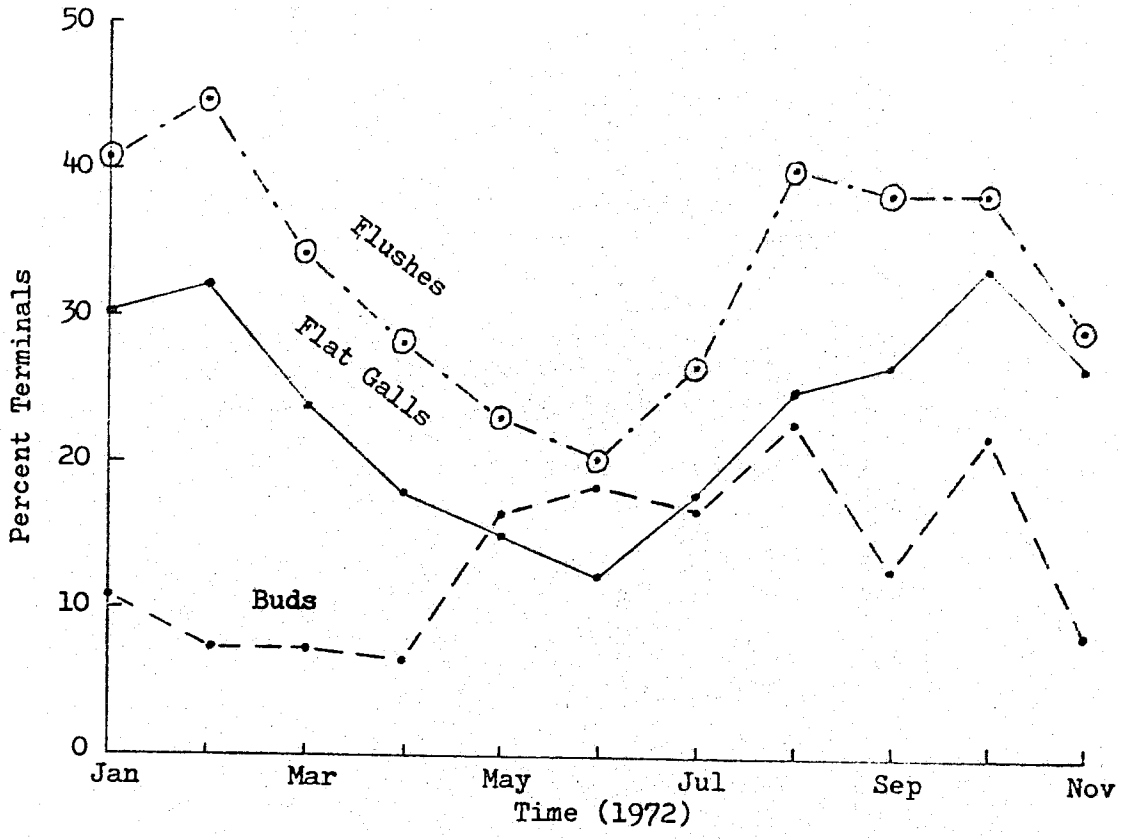

Figure 1. Metrosideros/psyllid relationship at 4000' elevation.

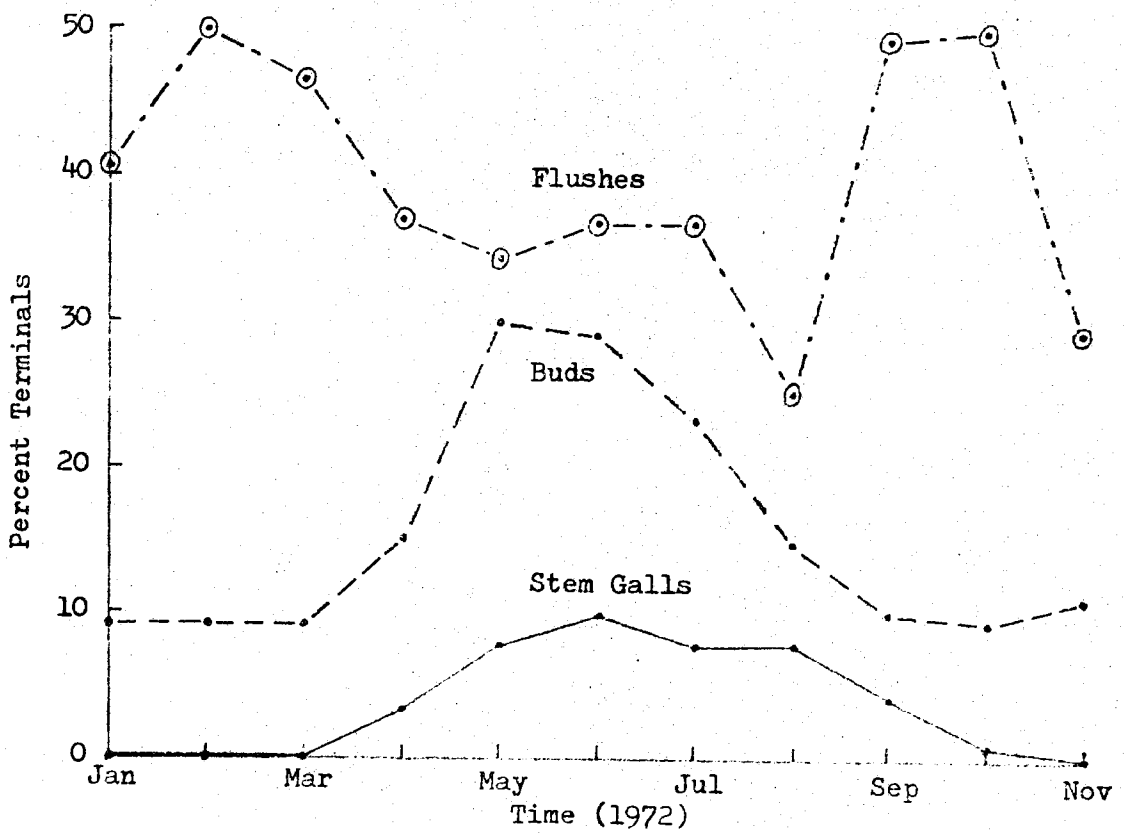

Figure 2. Metrosideros/psyllid relationship at 8000' elevation.

At 8000' peak budding is followed by a corresponding peak in stem galling. Stem galling is therefore highest during the summer months resulting in a higher population of adults during the cooler and wetter months. At the lower elevations, the peaks and troughs of stem galling are not as visible as those at 8000'. Other types of galls also may not display as definite a cyclic action at various elevations.

Table 1 shows that although the psyllids as a group may be predominant in certain areas, individual species have been able to find their own favorable niche along the transect gradient. The distributional pattern of the psyllid approximates that of Metrosideros showing a great adaptability of both to various climatic conditions. This relationship suggests a close evolutionary relationship between Metrosideros and the psyllid taxa.

Other data reveal that a favorable niche for the psyllid can further be found in only certain trees within a Metrosideros variety. Tree-to-tree differences in galling have been observed over a long period of time in the study areas. A polymorphic nature within the variety is suggested when trees of the same variety in the same area are either highly galled or have few or no galls during the course of a year.

Abiotic and biotic factors also create unfavorable conditions which work against the Metrosideros and psyllid phenology. Sunlight and rainfall may affect psyllid site selection and egg laying behavior as temperature and daylength are known to affect the life cycle. An anystid mite, neuropterans, nabids, coccinellids and spiders feed on the exposed nymphs and adults, while a eulophid, Pauahiana swezeyi Yoshimoto feeds on the nymphs within enclosed galls.

Studies on the psyllids' relationship with Metrosideros are continuing, and a comprehensive technical report on the subject will be published at a later date. The report will cover the description, abundance, and distribution of the above-mentioned pysllids.

Table 1. Indices of psyllid galling on Metrosideros on Mauna Loa Transect 1.

Elevation (feet)	Galling (%)*				
	Trioza n. sp. 1	Trioza n. sp. 2	Trioza hawaiiensis	Kuwayama minuta	Total **
4000	23.5	9.9	3.9	0.0	37.3
5500	17.3	0.0	0.0	0.0	17.3
6600	11.2	0.0	2.7	6.8	20.7
7000	1.0	0.0	1.7	12.0	14.7
8000	6.9	0.0	3.6	0.0	10.5
Average	12.0	2.0	2.4	3.8	

* Percentages of terminals with unopened galls. Based on average of monthly observations from January to November 1972.

** Relative abundance.

Progress reports on soil and duff inhabiting arthropods, vertebrate ectoparasites, and cavernicoles in lava tubes.

F.J. Radovsky
J.M. Tenorio
F.G. Howarth

This project has evolved through opportunity and the requirements of the Subprogram to encompass three essentially distinct areas of research. Each of these areas would qualify as a distinct project, but it is convenient for administrative purposes and because of the capacity for integration of field work to continue them as a single project.

Since funding of the project was initiated with the second year of the Subprogram, in September 1971, the major change has been to incorporate the work of Howarth on the cavernicolous biota of the Hawaiian Chain, which he discovered in July of 1971. Radovsky is acting in an advisory capacity for this part of the project and Howarth is organizing and conducting the research and publication. As indicated in the summary report on lava tube research that follows, the discoveries already made form a large body of new scientific knowledge; the significance of this area for future evolutionary and ecosystem research is of major importance.

The personnel organization of the soil zoology and ectoparasitology sections of the project remain nearly the same as given in last report. Tenorio is principal assistant to Radovsky and supervises laboratory processing and sorting of organisms. Jacobi is principal field technician. The mammal ectoparasite studies are fully integrated with mammal studies of P. Tomich (project D-2). Dr. Gordon Wallace has completed his related studies on toxoplasmosis in small mammals and is no longer actively participating in the project. Soil studies are now integrated with algal and fungal studies of Doty and Baker (projects B-7 and B-8, respectively). With respect to external collaborators working on identification of organisms, there have been two additions of particular significance to the project. Professor Janos Balogh of Budapest has visited the Bishop Museum, made initial studies on the Cryptostigmata (oribatid mites), and agreed to take full responsibility for identifications of this group. Secondly, R. Sims of the British Museum (N.H.) is providing identifications of earthworms.

A. Soil and Duff.

An initial Technical Report on soil arthropods will be completed during the first quarter of calendar 1973. It will be based on the results of collections through July 1972. Of the hundreds of species identified, data on distribution, abundance and seasonal cycles of more than 100 species at 14 sites (12 Mauna Loa Transects, 2 Kilauea Forest Reserve) have been tabulated and are ready for computer listing. This number excludes the important Cryptostigmata for which identifications and quantitation will be available soon. Detailed analysis will be concentrated on Collembola, Cryptostigmata, and Mesostigmata. The following generalizations can be made. (1) The dominant soil and litter mesofauna was poorly known prior to this study, as demonstrated by the high proportion of new records. (2) All groups of true cryptozoa include a high proportion of introduced or probably introduced species. (3) Species tend to be distributed over a wide range with regard to altitude, vegetation type, and soil type; however, clear p

patterns of habitat association are evident for a number of species. Reference to 21 species of Collembola selected as common forms in at least some habitats illustrate these generalizations: 62% are new records for Hawaii; a minimum of 76% are probably introduced species on the basis of their kn own distribution elsewhere (applies equally to species at 8,000 feet in almost exclusively native vegetation as well as those on more disturbed sites of lower elevations); 38% of the species were found in 11 or more of the 14 sites. The low level of endemics is one of the more interesting results, especially since foliar arthropods in the same habitats tend to include a high proportion of endemics. This suggests that an endemic insular soil fauna is more susceptible to disturbance and replacement by introduced species as a result of human activity. Such eurythermal and cold-tolerant species as Entomobrya nivalis are able to establish themselves as the dominant Collembola at higher altitudes. Studies on annual cyclical abundance lead to tentative conclusions that some species, particularly at higher elevations, have peaks of abundance during the warmer periods when generation times are shorter; while other species may be more closely dependent on rainfall (a possible artifact of earlier sampling technique that is being studied further).

During July and August of 1972, two basic changes were made in sampling. The locations of some of the 12 pitfall traps on the Mauna Loa Transect were changed to more closely correspond to primary IBP sites being used by others; at the same time the IBP primary sites were modified to some extent in order to correspond to the soil sampling locations. One of the Kilauea Forest Reserve pitfall traps was moved to a spot near the other and enclosed with a fence to exclude pigs; this will allow a measure of influence of pigs on the soil fauna and will integrate with the studies of pig effects on vegetation (projects B-1, B-2). The second major change was in soil-sampling procedure for Berlese-extraction of arthropods. Extracting two fractions in the first year, the litter layer and approximately 0.5 liter of surface soil from a 0.05 m^2 area, did not provide consistent results and yielded only a small fraction of the species represented in pitfall traps. We are now taking litter from a 0.25 m^2 area and taking 3 sub-litter core fractions each 3 cm in depth; the fractions from the same depths are combined from 4 corings and total 275 cc^3/extraction. Preliminary analysis indicates that this is providing a much improved measure of the total soil mesofauna at various levels. Subsamples of each soil fraction are used for algal and fungal studies at the same sites (projects B-7 and B-8).

During the next year biomass-studies will be initiated. Sampling will be extended to a variety of habitats that may act as reservoirs for endemic species, for example accumulation of soil and debris suspended in trees and other plants; pockets of soil and plant growth on lava flows; and collections from isolated forest areas that have been less subject to human disturbance. These findings with the results of collections at the primary IBP sites will relate to hypotheses being developed on the origin, evolution, and fragility of insular soil faunas.

B. Ectoparasites

From its inception, the method of recording mammal and ectoparasite data was designed to facilitate computer listing and analysis of results. All data have been computer-listed through September 1972, reorganized to facilitate further analysis, and partially analyzed. The results of this portion of the study will form a technical report to be completed during the first quarter of calendar 1973.

During the period through September 1972, 475 animals were washed by a standard procedure for recovery of ectoparasites. Collecting was carried out on 4 transects within the Kilauea Forest Reserve and on 9 trap lines from 2,900 to 7,000 ft on the Mauna Loa transect. The animals were Rattus rattus (219) Mus musculus (209), Rattus exulans (40), and Herpestes auropunctatus (7). This is the first detailed and long term study of ectoparasite populations on small mammals in Hawaii, both for a wet montane forest and over an altitudinal gradient. Distinct distributional variations in ectoparasites independent of host distribution are evident in a number of instances, and we are examining the factors contributing to these differences. Most unusual is the finding that 2 species of listrophorid fur mites are very sharply restricted altitudinally although the hosts are found at higher altitudes: Listrophoroides expansus found on both Rattus species and Listrophorus musculus found on Mus do not occur above 4,000 ft. although often very common at low altitudes. This situation is unexpected because the mites are permanent parasites on homeothermic hosts, and such parasites are normally independent in their range from ambient climatic conditions. There is a need for further research to determine if the parasites are excluded from higher altitudes because of direct sensitivity to the host's environment or in response to physiological differences in the hosts. New records are for Hypoaspis species and other mesostigmatic mites that are not true parasites, but rather nest predators and phoronts and scavengers on the host. Certain of these show consistent and regular host associations. Some of those recorded are undescribed species; one species (Hypoaspis nidicorva), found both on rodents and in litter, was previously known from a single collection in a crow's nest in England. We also examined the nasal passages and found 2 species of nasal mites (Ereynetidae) in Rattus and Mus, the first records of nasal mites for rodents in Hawaii.

The Mauna Loa Transect sites have been modified during the second year of studies on this transect. A regular collecting line has been set at 8,000 feet and intermittent trapping extended to 10,000 feet. Mus musculus has been captured at 9,500 feet. The collecting will be continued until 2 full years are completed in all areas (through October 1973 for the Mauna Loa Transect). Further studies will be conducted in other parts of the islands for comparative data on ectoparasites of small mammals; during the coming year and subsequently more emphasis will be placed on the ectoparasites of birds, especially the endemic avifauna.

Reference: Note on Hypoaspis nidicorva Evans and Till, 1966 as a new state, hemispheric, and host record by Radovsky and Tenorio. Proc. Haw. Entomol. Soc. (in press).

C. Cavernicoles in Lava Tubes (F.G. Howarth)

Since the initiation of this study more than 60 lava tubes have been investigated and notes on the biotic communities and environmental conditions made. The study is still in the survey or census-taking stage, as new organisms are still being discovered. The Hawaiian cave fauna is very disharmonic compared to continental cave fauna, and many organisms are real surprises. The first IBP technical report is about to be issued* and will also form the introduction to the series of published systematic papers on the fauna. The cave-adapted arthropods are being described by collaborating specialists as a series of papers published in Pacific Insects. Three of the systematic papers, with the introductory section, are in press. There will be approximately 12 papers in the completed series.

Faunistic surveys of new caves as they are found are still the major emphasis of this project. In this way many different types of caves in different environments and on different islands will be investigated to formulate ideas on the evolution of cave organisms and the ecology of the Hawaiian cave environment. Many caves, especially on the older islands are in jeopardy from development, agriculture, or other land use changes, and it is imperative that they be studied as soon as possible. Many potentially significant caves have recently been destroyed before they could be investigated.

The caves near or along the transects on Mauna Loa and Kilauea are being more intensively surveyed to correlate data on cavernicole distribution with that of the soil arthropod studies. Preliminary results of this show a remarkable lack of overlap between species collected by the soil arthropod group and those collected in the cave environment. The majority of species common in caves, even introduced soil species, are not found or are very rare in the soil. The reverse is also true. The arthropdds which are extremely abundant in the soil are rare accidentals or are not at all found in caves. If this observation is true, it will be important to understand some of the factors involved. Is there a clear division between those animals able to live in perpetual darkness without many environmental cues and those soil animals which require external stimuli for biological processes, such as reproduction, and daily and annual rhythms?

Kazumura Cave, Kilauea massif, between 250 and 450 m elevation, is being intensively studied. It is one of the longest lava tubes in the world, with more than 8 km of known passage. The ecosystem is richer and more varied and complex than that in other caves studied. A map of the cave is being prepared preliminary to a more detailed study of population dynamics and interrelationships of the cave animals with the cave and surface environment. This information will supplement the soil arthropod studies. A preliminary food web for Kazumura Cave was included in the technical report.

Lava tubes, unlike limestone caves, are relatively short lived, and the assumption has been that lava tubes are too ephemeral to contain specialized cave life. However, my study has demonstrated that young basaltic lava has numerous avenues such as vesicles, fissure, layers, and smaller lava tubes which allow some inter-lava tube and inter-lava flow dispersal of cavernicoles. Thus young lava tubes can be colonized by cave populations soon after the buildup of organic material allows establishment. This is a significant finding for it allows us to predict the existence of a cave-

*Technical Report No. 16

adapted fauna in any volcanic area with numerous lava tubes and continuous volcanism over a long period of time and with environmental conditions favoring their colonization.

The discovery of troglobites (obligatory cavernicoles) among representatives of the adaptively radiating fauna on oceanic islands will surely lead to a better understanding of evolution on islands, in caves, and in general. For example, Hawaiian caves have been invaded by representatives of some of the successfully speciating groups by a process of adaptive shifts. This suggests that troglobites become relicts only after the extinction of surface populations, not that they become cave-adapted after extinction of the surface populations, the accepted paradigm of many cave biologists elsewhere (see Barr, T.C. 1968. Evolutionary Biology Vol. 2, 35-102).

Dr. Ellysse Craddock conducted a preliminary study of the cytogenetics of the two cave species of Caconemobius crickets. I supplied her with approximately 10 crickets of each species. These were from one cave on Maui and 2 caves on Hawaii. She has now left the islands but hopes to report on the material she has.

The cave populationslend themselves beautifully to a variety of cytological and genetic experiments. It may be possible to discern the degree of isolation between cave populations, and also the amount of change between a cave population and its epigean (surface) relatives.

The recent realization by the Volcano Observatory staff of the significance of lava tubes in the building processes of shield volcanoes has given new impetus to the study of lava tube formation by that staff. It will be possible for us to coordinate our work and integrate the study of the geology of lava tube formation and cave ecology. This is still in the planning stage, however.

Significant observations incidental to the primary goals of this study are being made on nesting of native birds in the twilight zone of lava tubes and the presence of avian subfossils in lava tubes (integrated with project D-1).

Publications:

Fennah, R.G. 1973. The cavernicolous fauna of Hawaiian lava tubes, Part IV, Two new species of cavernicolous Oliarus (Cixiidae) from the Hawaiian Islands. Pacific Insects 15(1): in press.

Gertsch, W.J. 1973. The cavernicolous fauna of Hawaiian lava tubes, Part III, Araneae. Pacific Insects 15(1): in press.

Howarth, F.G. 1972. Cavernicoles in lava tubes on the island of Hawaii. Science 175: 325-326.

_____. 1973. The cavernicolous fauna of Hawaiian lava tubes, Part I, Introduction. Pacific Insects 15(1): in press.

Schultz, G.A. 1973. The cavernicolous fauna of Hawaiian lava tubes, Part II, Isopoda. Pacific Insects 15(1): in press.

Titles of papers given at scientific meetings:

Howarth, F.H. 1972. Hawaiian Lava Tubes: A Preliminary Report. Vulcanospeleology Symposium: National Speleology Society Convention, White Salmon, Washington. August 16, 1972.

_____. 1972. The Fauna of Hawaiian Lava Tubes. Biology Session: Same Convention.

Other grant support:

A grant of $100.00 was received from the Research Advisory Committee of the National Speleological Society to publish the introductory paper.

Collaborating specialists:

Arachnida	- Araneae	- W.J. Gertsch
	- Acarina	- F.J. Radovsky, et al.
Crustacea	- Isopoda	- G.A. Schultz
	- Amphipoda	- E.L. Bousfield
Diplopoda		- N.B. Causey
Insecta	- Collembola	- P.F. Bellinger
	- Thysanura	- P. Wygodzinsky
	- Orthoptera	- A.B. Gurney, D.C. Rentz
	- Dermaptera	- F.G. Howarth
	- Hemiptera	- W.C. Gagne
	- Homoptera	- R.G. Fennah
	- Coleoptera	- G.A. Samuelson, E.C. Zimmerman
	- Lepidoptera	- D.R. Davis
	- Diptera	- W.A. Steffan, D.E. Hardy, J.M. Tenorio, et al.

Progress Report on Insect Interference in the Reproductive Cycle of Community Structure Forming Plants, Particularly Seed Feeders

W. C. Mitchell
B. M. Brennan

A preliminary list of the insects associated with Metrosideros collina polymorpha (Gaudichaud) and Acacia koa Gray has been compiled. Swezey (1954), in his Forest Entomology in Hawaii, listed 154 insects associated with A. koa Gray and 96 associated with M. collina polymorpha (Gaudichaud). This has been expanded to 204 and 134 species respectively. There is an exchange of information and cooperation with the scientists on Hawaii IBP projects C-4, C-5, and C-6 that are studying various aspects of the insect fauna of ohia and koa. This project is limited to the insects that are associated with flower development and seed production.

Insects associated with the blossoms and developing seed of ohia (Metrosideros sp.) have been collected along the Mauna Loa transect at IBP Site #3 (4000' elevation; Site #7 (5650' elevation); Site #9 (6700' elevation); Site #10 (7000' elevation) and Site #13 (8000' elevation). Insects were collected from blossoms with a portable vacuum cleaner modified for field use. Insects collected in the preliminary samples included Thysanoptera, Hymenoptera, Hemiptera, Diptera and Acarina. These samples were collected during November and December. At each elevation observations were made concerning the abundance of blossoms, selected climatological conditions, and insect activity.

Developing seeds were collected from the same trees from which blossoms were sampled. These were processed through a Berlese funnel. Preliminary inspection indicated the presence of Hemiptera, Dipterous larvae, mites and spiders. Acacia koa Gray blossoms collected at IBP Site #4 (4200' elevation) and Site #9 were also processed through a Berlese funnel.

In 1973 attempts will be made to collect insects with weather vane traps equipped with sticky boards. The primary insects associated with each stage of plant reproduction will be determined.

LITERATURE CITED

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C-12

M. Tamashiro
M. Conant

Progress report on effects of diseases of insects in Hawaiian ecosystems

This study has been concerned with determining the life-cycle of Uresiphita polygonalis and the distribution and parasites of the larvae.

The life cycle of Uresiphita polygonalis does not appear to have a diapause. Breeding continues throughout the year. Eggs and larvae of different ages can be found on Sophora foliage throughout the year on Mauna Loa and Mauna Kea. Generations require about 50 days and overlap.

Population samples were taken at monthly intervals from May 1971 to July 1972 with records being kept of the number of caterpillars on the trees and causes of deaths occurring during the larval and pupal stages. These records show the trends listed in the following paragraphs.

Four species of parasites of Uresiphita polygonalis have been recorded from Mauna Loa and two species of parasites have been recorded from Mauna Kea near Kilohana. Two of the parasitic species from Mauna Loa, one an egg parasite and the other an internal larval parasite, were collected only twice. Populations of U. polygonalis at the same elevations at both locations are approximately as dense.

The two common species of parasites are a tachinid fly, Lespesia archippivora, and a wasp, Horogenes blackburni. There has been some difficulty in comparing the abundance and composition of parasites at Mauna Loa and Kilohana because most U. polygonalis larvae collected near the Kilohana area die of a virus disease before parasites can emerge.

At 4,300 feet on Mauna Loa the greatest numbers of caterpillars were found in the middle of June in 1971 and at the end of April in 1972. The frequency of parasitization by the wasp, Horogenes blackburni, peaked in the beginning of June 1971 and held until the end of that month. In 1972, the wasp numbers peaked and held throughout June. The frequency of parasitization by the tachinid, Lespesia archippivora, peaked in the middle of June in 1971 and in the beginning of June in 1972.

At 5000 feet the greatest numbers of caterpillars are found in April; these rapidly decrease in June and July. At this elevation, the greatest percent parasitism by H. blackburni and L. archippivora was found in the beginning of May, continuing through June and rapidly decreasing in July.

The most striking differences in magnitude of population fluctuations of U. polygonalis and its parasite, H. blackburni, occur at 6700 feet. At 6700 feet the greatest number of caterpillars were found during the beginning of July in 1971 and the beginning of June in 1972, with both rapidly decreasing in the following weeks. In 1971 and 1972, H. blackburni parasitism peaked in the beginning of July. Only one tachinid parasite was collected from larvae at this elevation and that was in the beginning of July, 1972.

On Mauna Kea on the Saddle Road near Kilohana at approximately 5400 feet

elevation, the larval population of U. polygonalis peaked in mid-June, 1971 and in the beginning of June 1972. The larvae died rapidly from a virus when they were removed from their natural location or if their environment on the tree was altered (e.g., placing a barrier to contain larvae on a portion of the tree), making frequency of parasitism difficult to determine.

A histological examination of diseased larvae is underway. The results of this examination will be reported in detail at the conclusion of this subproject.

This study will be completed by June 1973. The results will be available in a M.S. Thesis by M. Conant.

D-1

Progress report: Life history and evolution of the Hawaiian honeycreepers.

A. J. Berger
R. E. MacMillen
R. J. Raikow
Walter Bock
Sheila Conant

Two technical reports were completed and distributed during 1972.

1. Ecological and biological studies.

The discovery during the past year of previously unreported phenomena exhibited by endemic forest birds (see Technical Reports nos. 8 and 11) suggested new aspects of ecological relationships to be studied. This phase of the work is now being pursued intensively by Dr. Sheila Conant, a post-doctoral fellow as of September 1972. During the coming year, she will be able to check the results of my preliminary census data in Volcanoes National Park and the Kilauea Forest Reserve and will be able to expand the scope of the ecological study. She also will put in use a recently acquired detecting sensor camera in an attempt to document photographically predation by rats on the eggs, young, and adult birds of the Hawaiian rain forests (I obtained considerable circumstantial evidence for this predation previously, but without positive proof).

During the current breeding season, I plan to obtain egg albumen from endemic bird eggs to send to Dr. Charles G. Sibley of Yale University for electrophoretic analysis; the results will aid in determining phylogenetic relationships of the Drepanididae.

2. Physiological ecology studies.

Dr. Richard E. MacMillen conducted thermoregulatory experiments with my captive Nihoa Finches (Psittirostra cantans ultima) during the summer of 1972, thus extending this work to include three species of honeycreepers. (Amakihi, Loxops virens, and Anianiau, L. parva). His data reveal unexpected differences between the honeycreepers and continental passerine species studied previously (see his report, D-3). It is very important to extend this work to include representatives of the second subfamily of honeycreepers (Apapane, Iiwi), in part, because of evolutionary implications. Dr. MacMillen's efforts (December 27, 1972 - January 2, 1973) to capture these species on Hawaii and return them to my aviaries in Honolulu were unsuccessful, and we have discussed an alternative plan for his work in Hawaii during the summer of 1973.

3. Functional anatomical studies.

Dr. Robert J. Raikow is continuing his research on the muscular system of the honeycreepers. This is a far more complicated project than that simple statement suggests, however. So little is known about the complete appendicular myology of passerine birds that it is essential for

Dr. Raikow to analyze the muscular patterns in a wide variety of other passerine families that could have provided the ancestral colonizer that evolved into the present-day honeycreeper family. Only with this background available can meaningful comparisons of the musculature be made. Similarly, I am continuing my study of the pterylosis of the honeycreepers.

Dr. Walter Bock of Columbia University is continuing his studies of jaw musculature of the honeycreepers and other passerine families.

Hopefully, we will by June 1974 have enough data on different anatomical features to serve as a far better basis than previously available to discuss the possible ancestors of the Drepanididae as well as relationships within the family.

4. The evolutionary study: a problem.

The laboratory studies and the field investigations on the island of Hawaii present no problems. To gather field data that are essential to unravelling the relationships within the family Drepanididae and their relationships to other passerine families, however, intensive field work must be conducted in two areas that provide habitat for species that are not found on any other island: (1) the windward slope of Mt. Haleakala, Maui, and (2) the Alakai swamp of Kauai. Virtually nothing is known about the distribution, population size, annual cycle, or breeding biology of a single species of endemic bird found in these areas (the single exception being that John L. Sincock found the first nest for the Kauai Oo during 1971). Unfortunately, the State Department of Land and Natural Resources has refused to grant the Hawaii Island Ecosystems Stability and Evolution subprogram permission to construct adequate cabin shelter in either of these areas. The terrain is extremely rough and treacherous in both, and the climatic conditions are rigorous (from about 300 to more than 400 inches of annual rainfall and winter temperatures down to 45° F and lower at night). A warm, dry cabin at night is essential for both personnel and expensive equipment in such regions. Unless this situation is rectified, personnel of the Hawaii IBP subprogram cannot conduct their coordinated studies as they know they must in order to interpret the many ramifications of island ecosystem analysis.

D-1

Sheila Conant
A. J. Berger

Progress report on gradient analysis of the avian community

The gradient analysis studies of the avian community have been in progress only since September 1972, so that insufficient data are available for analysis at this time. There are some new observations on the distribution and behavior of several species, however, which are pertinent for reporting.

On 17 October 1972, Conant observed two thrushes (Phaeornis o. obscurus) attempting to copulate in the top of a tall (35 m) dead ohia tree in the Kilauea Forest Reserve about 0.25 miles north of the IBP climatic station. On 5 January 1973, in the Kilauea Forest study plot near the start of transect 1, a pair was observed engaging in mutual preening (allopreening), and one of the birds exhibited what appeared to be courtship feeding solicitation display.

Conant has confirmed James Jacobi's sighting of the thrush at high altitudes. On 27 October 1972 James Jacobi, Dr. P. Quentin Tomich and Conant were returning from Puu Ulaula (10,000 ft.) on Mauna Loa. They heard thrushes calling infrequently beginning just a few hundred yards away from the Puu Ulaula cabin to a point between the 8,000 to 7,000 ft. markers on the trail. At 8,500 ft., two adult and one juvenile thrush were observed. No evidence of nesting was found, however. Jacobi has made additional sight records of thrush at and above 8,500 ft. and one at 6,900 ft. along the Mauna Loa Transect.

On 6 December 1972, Conant made several observations suggesting that nesting activity was imminent for three species of honeycreepers and the elepaio (Chasiempis s. sandwichensis). Apparent territoral encounters between three pairs of elepaio were noted at different places in the Kilauea Forest study plot. The encounters included excited chatter, singing and fights involving body contact. In a study of the Oahu elepaio (C. s. gayi, Frings 1968), such territorial displays were uncommon except during the breeding season. A pair of creeper touched mandibles, (Loxops maculta mana), as in courtship feeding; and a pair of akepa (Loxops c. coccinea) engaged in courtship feeding; twice the male appeared to feed the female; both times the female fluttered her wings briefly.

On 4 January 1973 Rick Warshauer observed an apapane carrying nest material at the west edge of the Kilauea Forest Reserve about 0.75 miles south of the IBP climatic station.

On 8 January 1973 Terry Parman saw an adult iiwi (Vestiaria coccinea) feed another adult iiwi a reddish-orange berry, possibly pilo (Coprosma rhynchocarpa). The bird receiving the berry crouched and fluttered its wings.

The akiapolaau (Hemignathus wilsoni) has been the subject of perhaps the most interesting observations of birds in the Kilauea Forest Reserve. James Jacobi observed an akiapolaau that appeared to feed another akiapolaau on 22 July 1972. He felt that the bird being fed was a fledgling, but could not be sure. He made a similar observation on 23 October 1972, this time describing the bird receiving food as definitely fledgling-like in appearance and behavior. The next day Conant observed two adult and one fledgling akiapolaau on the logging road near the beginning of transect 1. The young bird was olive drab, much duller in color than either adult; its plumage was ragged and the lower mandible was cream colored, whereas in the adult the lower mandible is black. The fledgling gave a high-pitched cheep

and fluttered its wings frequently while following the adults, which fed it about once every two or three minutes. Jacobi confirmed that the birds he had observed the day before behaved similarly.

On 18 January 1973 at about 1200 ft., Paul Banko, James Jacobi, Terry Parman and Charles Van Riper found the first akiapolaau nest ever recorded; the nest was under construction in an ohia tree on the trail between the ends of transects 3 and 4. They observed the birds adding material to the nest for about an hour; the following morning, the birds added material about once every 20 minutes for two hours. Unfortunately, the nest was inaccessible for marking and photographing eggs and young.

All of these data suggest that the akiapolaau breeds during the months from June through January or February.

Two introduced species of birds were recorded in the Kilauea Forest study plot for the first time. On 22 November 1972, Conant saw a pair of Cardinals (Richmondena cardinalis) about 20 m west of plot 1 on transect 1 in the study area, and on 12 December 1972, two laced-necked doves (Streptopelia chinensis) were seen near the end of the logging road between transects 2 and 3.

D-2

Progress report on small mammals — P. Q. Tomich

a) Population Characteristics of Introduced Rodents and Carnivores in an Island Rain Forest

Field work continues with bimonthly sampling of the four transects of the Kilauea Forest Reserve study area (two transects per month). Trapping will terminate in June, 1973 when two complete years of data will have been collected.

The roof rat remains the prominent species in the forest and yields information adequate for extensive computer analysis. The mongoose is common; the house mouse, feral cat and Norway rat are scarce.

This study is closely correlated with C-9 (F. J. Radovsky) and provides host animals for these ectoparasite studies.

b) Habitat, Climate and Altitude as Factors Affecting Introduced Small Mammals of the Mauna Loa Transect

We are now in a second year with a principal investigation of 14 sampling sites ranging from 3,000 to 8,000 feet elevation. Lesser effort is being applied to four additional sites to 10,000 feet. We are trapping only for rodents and find the roof rat, Polynesian rat and house mouse variously abundant along the transect.

The field phase will terminate in September, 1973, at the end of two full years. We anticipate that the results of the study will explain the ecological position of the several rodents, especially as related to environmental gradients. This work is also closely integrated with C-9 (F. J. Radovsky) in studies of ectoparasites.

c) Food Preferences of Introduced Murine Rodents in Native Forest Ecosystems

Stomach contents of rodents autopsied in the work at Kilauea Forest and on the Mauna Loa Transect have been routinely preserved since the inception of these projects. Arrangements have been made just recently with the phenological group (B-3, J. R. Porter) to analyze and report on these materials. Thus, the objective of integrating the study of the rodent foods with data on seasonal availability of these foods, is being met. Animal matter will be treated by appropriate specialists.

All data on the small mammals have been carefully coded for machine processing and cannot be handled realistically without programming assistance. Action in this area is a number one priority. Results of the first year of field work have been punched but we have not received the preliminary sorting and tabulations requested. June, 1973 is set as a time for completion of programming. Preparation of Technical Reports is scheduled to be completed before June, 1974. Preparation of papers for publication is anticipated in FY 75.

D-3

Progress report on the physiological ecology of some terrestrial Hawaiian birds and mammals

R. E. MacMillen

Work completed in FY 72

The months of July and August 1972 were spent on the subproject working mostly in the laboratory of Dr. G. C. Whittow, Department of Physiology, School of Medicine, University of Hawaii. During this period a manuscript was prepared entitled "Bioenergetics of Hawaiian honeycreepers: The Amakihi (Loxops virens) and the Anianiau (L. parva). This subsequently has been released as Island Ecosystems Technical Report No. 9, and it has also been accepted, subject to minor revision, for publication in Condor.

In addition to the preparation of a manuscript, extensive laboratory investigations of the bioenergetics of the Nihoa Finch, Drepanididae: Psittirostra cantans, were completed. These studies, conducted on a captive colony maintained by Dr. A. J. Berger, included measurements of oxygen consumption, evaporative water loss, body temperature and ambient temperature. The data are presently being analyzed statistically, and an additional Technical Report and manuscript to be submitted for publication will be forthcoming. In addition, five days (18-22 July 1972) were spent in the vicinity of the Kilauea Forest Reserve, Island of Hawaii, observing behavior, feeding activity, and flight patterns of Hawaiian honeycreepers, particularly those of the Amakihi (Loxops virens), the Apapane (Himatione sanguinea), and the Iiwi (Vestiaria coccinea). Accompanying me on this field excursion were Dr. A. J. Berger and Mr. E. A. Christopher (my research assistant).

Work completed and projected for FY 73

An excursion was made to the vicinity of the Kilauea Forest Reserve, Island of Hawaii, between 27 December 1972 and 4 January 1973 for intensive field observations of the birds to be studied in the laboratory during the summer 1973 and winter 1973: the Apapane (H. sanguinea) and the Iiwi (V. coccinea). Large numbers of these birds were observed, and also of the Amakihi (L. virens). The observations revealed much about the seasonal availability of the species, and suggestions concerning their energy relations in the field.

During July 1973 I plan to establish a laboratory at Volcanoes National Park to conduct bioenergetic studies of the Apapane. My observations suggest that these delicate birds can be captured by mist-netting, removed directly to the laboratory for measurement, and then released within 24 hr. of capture without harm. Observations during December 1972 and January 1973 indicate that neither freshly captured adult Apapane nor Iiwi can be held in captivity for more than 48 hr. without harmful effects. The month of August 1973 will be spent in Honolulu, statistically analyzing the data collected to date, and in the preparation of manuscripts.

This winter (1973) a second major project will be undertaken conconcerning thermoregulation and water relations of the Polynesian rat (Rattus exulans). Dr. P. Q. Tomich (pers. comm.) has demonstrated that the distribution of this rodent is restricted to lowland situations, generally below 4,000 ft. in elevation. Since the major environmental variable that is correlated (indirectly) with altitude is temperature, the distribution of R. exulans suggests that they are intolerant to the low temperatures of higher altitudes, and likely experience thermoregulatory

failure or impairment. The initial studies will consist of measurements of metabolism and thermoregulation in response to a range of environmental temperatures, with emphasis on low temperatures. In addition, over the next two years a study of salinity tolerances and water requirements will be undertaken in R. exulans. These data should reveal whether dispersal throughout the Polynesian islands was facilitated by unusual tolerances of saline-water utilization (sea-water drinking) or water restriction or deprivation. The work on R. exulans will be conducted during the academic year at my home institution, University of California, Irvine. A captive breeding colony of R. exulans is presently being maintained in my wild animal facility on the Irvine campus.

Work projected for FY 74

A. Up to June 1974 - I will plan to establish laboratory facilities again at Volcanoes National Park in January 1974 to conduct bioenergetic studies of the Iiwi, Vestiaria coccinea. This delicate and rather rare species is too dispersed for successful collecting during the summer (pers. obs.). However in winter individuals are concentrated in the vicinity of flowering mamani (Sophora chrysophylla) trees at elevations between 5,000 and 6,000 ft. (pers. obs.). They feed actively on mamani flowers, and can be collected fairly readily. During this winter (December 1972, January 1973), trial netting captured eight Iiwi in a four-day period, indicating that samples sufficient for this proposed experimental work can be obtained readily.

   By June 1974 (termination of IBP) I will have basic information on energy metabolism, thermoregulation and evaporative water loss in five species of drepanidids, representative of divergent phylogenetic stages of the two subfamilies: Psittirostrinae - Loxops parva, L. virens, Psittirostra cantans; and Drepaniinae - Himatione sanguinea, Vestiaria coccinea. Such information will reveal, as was originally proposed, the extent of physiological convergence on and/or divergence from mainland passerines of similar sizes, habits, and habitats. In addition, I will have determined the energetic responses of each of these species to the environmental temperatures to which they are exposed both seasonally and daily.

B. Beyond June 1974 - The major bioenergetic phenomena which remain uninvestigated are related to energy availability in the environment and comparisons of resource allocation between potential competitors, food niche dimensions, and energy conversion efficiencies.

   Drs. Sheila Conant and A. J. Berger have proposed to study other aspects of honeycreeper community structure. I wish to study those aspects of drepanidid community ecology that are particularly related to the above-mentioned energetic components, which, when assessed in light of the previously-conducted laboratory studies of energetics, will reveal much valuable information concerning the roles of honeycreepers in the trophic structure of, and energy flow within, this island ecosystem.

   I am proposing that one of my colleagues here at University of California, Irvine, Dr. F. Lynn Carpenter, a community ecologist with special interests in avian energetics collaborate with me in these

studies as co-investigator. I have included requests in the budget for FY 74 for return transportation for Dr. Carpenter, Los Angeles-Hilo-Honolulu, for both January 1974 and summer 1974, as well as summer salary for Dr. Carpenter for two months in 1974, the times in which these studies will occur. In that academic commitments restrict research activities on this project to a maximum of one month in the winter and two in the summer, a full-time effort by a minimum of two individuals is absolutely essential for completion of this vital and culminating phase of the project. Dr. Carpenter and I have had the experience in related research activities to best ensure success of the proposed work. During January 1974 while I am completing the laboratory studies of the Iiwi, Dr. Carpenter will commence the field studies of community energetics. During the summer 1974, both Dr. Carpenter and I will continue and complete the field studies.

We will concentrate our efforts on the three most common honeycreeper species in the vicinity of the Kilauea Forest Reserve and the Keauhou Ranch, Island of Hawaii: The Amakihi (Loxops virens) and the Apapane (Himatione sanguinea) and the Iiwi (Vestiaria coccinea). The food habits of these birds have been investigated rather extensively previously (Baldwin, A. H., 1953. University of California Publ. Zool. 52: 285-298). We will augment this information by observation of feeding sites to determine the extent of resource competition in terms of temporal, spatial, and food species overlap. It is already known that the Amakihi restricts its activity to twigs and branches within and under the forest canopy, while Apapane and Iiwi are active on the canopy (Berger, A. J., 1972; Technical Report No. 11). Careful observation should reveal whether there is further resource division between these latter two species. In addition, we wish to apply a vomit-inducing chemical to newly netted birds to determine resource utilization both qualitatively and quantitatively. This chemical has been used on Oregon Juncoes without harm by Ms. Jennifer Meux White, University of California, Berkeley. Also, experimental procedures appropriate for field manipulations will be devised to determine the extent to which nectar is employed as an energy source. This will have to be determined indirectly by measurement of nectaries before and after avian use, since nectar is virtually impossible to determine and analyze in stomachs.

Because breeding is energetically crucial, the food fed to the young will be determined as an important key to niche overlap and interspecific competition. Time and activity budgets will be estimated to determine the amount of energy that the population of each species requires.

Conversion efficiencies for each species will be determined once the major resources are identified. This will consist of calorimetric determination of the foodstuffs (by bomb calorimetry), and of fecal material, to determine interspecific capacities for energy extraction from foods. Once energetic demands, efficiencies, and pattern of resource utilization have been determined for each species, we can study pollination strategies for the major plant species employed (particularly Sophora chrysophylla and Metrosideros collina) according to the ideas proposed by Heinrich and Raven (1972, Science, 176: 597-602). For example, a plant must maintain a balance between attracting pollinators with its rich and/or copious food sources (pollen, nectar)

and encouraging pollen dispersal by restricting the amount of food provided. Pollen dispersal can be measured by dyeing pollen grains and tracing their movements and the means by which they are moved. This will help determine the role and efficiency of honeycreepers as pollinators.

These data will provide: 1) quantitative and qualitative information on energy input and output as reflected in the resources that are available and utilized; 2) information on the intensity of competition for energy resources and; 3) values for relative energy demands and efficiency of energy utilization among the different honeycreeper species. These data will then provide meaningful bases for further interpretation of the laboratory data on energetics which will have been gathered previously. Together with the information on pollination, we hope to draw a comprehensive picture of energy flow and utilization of these important consumers in the island ecosystem, and their roles in the reproduction of some of the producers.

The increased budgetary requestes for the fourth year (1 September 1973 - 31 August 1974) reflect the inclusion (summer salary) of Dr. Carpenter as co-investigator on the project, without whose aid and expertise the project cannot be completed within the time schedule. A slight budgetary increase is also accrued by the necessity for field and laboratory work both in midwinter and mid-summer, requiring some additional travel from the mainland.

6.53

E-1

Progress Report on Genetic variations of Hawaiian Drosophila immigrans

Yong K. Paik
Kee C. Sung

A report entitled "Ecogeographical variations of chromosomal polymorphism in Hawaiian populations of Drosophila immigrans is going through the press for the IBP Technical Report #12. Two versions of this study have been published in abstract form in Drosophila Information Service (1972) and the full text of this study has been submitted to Genetics for publication. In this study, special emphasis was placed on work along Mauna Loa transect at five sampling stations from 4,000' to 6,700 '.

Up to date, it has become apparent that Drosophila immigrans breeds in the Mauna Loa transect up to the 7,000' level. We are planning further collections of this species even above this level in order to clarify the range of its vertical distribution. In the collections made in early April and late December of 1971, sampling was undertaken at 5 stations from 4,000' to 6,700' levels. In both collections, Drosophila immigrans was taken in large numbers and made up at least 70 to 80% of the total flies captured. Drosophila simulans was second in abundance (10 to 20%) and other exotic Drosophila species were absent except for the occurrence of Drosophila busckii at the 5,100' sampling site. By contrast, in our recent collection conducted in mid-October of 1972 Drosophila simulans was taken in tremendously large numbers and made up 50 to 96% of the total collections. Drosophila immigrans was second in abundance (3 to 40%) and Drosophila sulfurigaster, a species not found in the 1971 collections, was captured, but not in large numbers. In the 1972 collection, 4 sampling sites were added between 4,000' and 6,700' levels and another site at 7,000' was added. D. simulans, D. immigrans and D. sulfurigaster occurred throughout the entire range. Whether the shift in taxa or its relative abundance is correlated with the changes due to seasonal fluctuation in the same area is an open question, which can be settled only by further studies.

We were able to show from the studies of April and December samples of 1971 that a sharp shift has taken place with respect to relative frequencies of chromosome inversions between 4,000' and 5,100'. At the present time the significant heterogeneity between the two elevations appears to be due to the operation of differential selection on the different gene pools in two locations on the Mauna Loa transect. It turned out from the study of the October samples of 1972, however, that frequencies of chromosome inversions have shifted significantly in both elevations. Whether these frequency changes are due to seasonal fluctuations of the environment in the two parts of the transect or due to some other events is an open question. The answer to this question will be sought by further studies.

Attempts are being made to account for the differences in frequencies of inversions between the elevations and between seasons according to certain environmental parameters. Mr. Sung is successfully isolating from the Mauna Loa populations homozygous strains for inversions, and is about to begin a series of selection experiments in artificial population cages. It is hoped that the results will provide information as to the nature of differences between the

populations with regard to the frequencies of chromosome inversions. Parallel to his experiment, the principal investigator will run another series of experiments which are directed toward the determination of the ability of flies having various genotypic combinations of gene arrangements to withstand the stresses of several environmental factors. These will include stresses of high temperature, desiccation and/or low oxygen tension. The results will then be correlated with the characteristics of inversion polymorphisms observed in the different populations of Mauna Loa transect.

In conjunction with the study of genetic variations of this species in Mauna Loa transect, the genetic variability of Drosophila species will also be studied in Kilauea Forest Reserve. These comparative data will provide a more comprehensive picture of the genetic variations in the various ecosystems being studied by the IBP project.

During the early part of 1974, the Drosophila species will be studied for the incidence of visible mutations in different ecosystems on Mauna Loa transect and in Kilauea Forest Reserve. These data may supplement answers to the question, "Is the integration of this non-speciating Drosophila fly into different ecosystems associated with genetic changes?".

Continuing studies on
Hawaiian Drosophila species

W. W. M. Steiner

Of importance to the understanding of the stability of genetic systems is how changes in the environment may affect such stability. Few good studies exist which demonstrate a clear relationship between the two. Although evidence is accumulating that some electrophoretic gene markers display either clines or cycles, these have at best been only suggestive as to which particular environmental parameters are involved (Koehn and Mitten, 1972, Lakovaara and Saura, 1971, Tamarin and Krebs, 1969).

Theoretically, the monitoring of genetic and environmental changes over sufficient periods of time may provide insight into what components of an ecosystem may be interacting with a specific genetic system. The questions we may ask concerning these phenomena are relevant to objective four of the Hawaii IBP:

(1) Do clines or cycles in gene frequencies occur in Hawaiian species?
(2) If they do, what are the environmentally related parameters contributing to these? What is the mode of action of these parameters and the nature of the interaction involved?
(3) Of what importance are such genetic shifts to a species ability to adapt and evolve?

Because short-term genetic changes may reflect seasonal heterogeneity, these necessarily must be differentiated from long-term changes. A shift in gene frequencies of the latter type suggests changes may be taking place within a population's gene pool which may have far-reaching evolutionary consequences.

The examination of these questions requires more than just a single approach. We are attempting a multiple analysis technique on two defined populations of the endemic species Drosophila mimica and its sympatric species, Drosophila engyochracea. We will establish the population structure of these species through study of the allele frequencies at a series of electrophoretic loci. We will then be able to:

(1) Compare the data to those obtained by Rockwood (1969) to determine if genetic changes have occurred at the polymorphic loci she studies (acid phosphatase, octanol dehydrogenase and alkaline phosphatase);
(2) Establish gene frequencies at other polymorphic loci;
(3) Correlate gene frequencies with IBP meteorological data and correlate average genetic heterozygosity with seasonal heterogeneity.

If we assume that environmental moisture levels are an important parameter in certain Hawaiian ecosystems, by coupling the techniques of electrophoresis and dessication we may be able to provide direct evidence of selection at specific loci or linkage groups. Adaptation to this parameter should be particularly important for the Hawaiian Drosophilidae (see Carson et al., "Evolutionary Biology of the Hawaiian Drosophilidae," 1970, for a review). In order to investigate biological correlations to

relative humidity we have recently developed a desiccating apparatus (details to appear in Drosophila Information Service, volume 49, in press). We will study survivability of D. mimica and D. engyochracea under varying humidity regimes and:

(1) Electrophorese desiccated Drosophila and correlate genotypic variation to survival time;
(2) Establish relationships between an individual's heterozygosity estimate and its survival time and
(3) Conduct selection experiments using the larval stage to establish at what stage of development environmental moisture levels may be most selective.

Preliminary data has been obtained for D. mimica indicating that the alkaline phosphatase locus has a long-term stability, maintaining 4 alleles at 10% or higher gene frequencies. In addition a cyclical change at the 3-allele acid phosphatase locus has been observed. The correlation of this change with season (or possibly moisture) is being examined. A technical report is being planned which will report the details of these findings.

In addition, survival under desiccation suggests that slight adaptive differences between Kipuka Puaulu and Kipuka Ki populations of D. mimica exist. Further research is currently being conducted and will be the topic of another technical report. These findings will be submitted for presentation at the First International Congress of Systematic and Evolutionary Biology to be held in Boulder, Colorado, in August, 1973. The bulk of this work will comprise a Ph.D. thesis to be submitted to the Department of Genetics in approximately August, 1974.

It is hoped that the preceding studies will demonstrate which portions of the genome of a species change under adaptation and which are stable with respect to a common environmental parameter. From such data as this, evolutionary implications may eventually be drawn. These studies do not, however, demonstrate adaptability of introduced or non-endemic species. The question seems to be a paramount one in modern ecological studies, particularly where colonization of cosmopolitan or "weed species" has led to replacement of endemic ones. For this reason, we thought it would be of interest to compare the genetic structure of the locally widespread cosmopolitan, Drosophila simulans, with that established by continental American studies (O'Brien and MacIntyre, 1969; Berger, 1970). Samples taken at 5 elevations have been analyzed and will be dealt with in a forthcoming technical report. These studies demonstrate wider genetic variability than previously found. Whether this reflects a local condition or one which has failed to be detected in other studies is not presently clear.

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Preliminary report on electrophoretic variation in *Acacia koa*

W. W. M. Steiner

The first major objective of the Hawaii IBP, to determine why some organisms in Hawaii have undergone speciation while some of the most successful have not, was originally thought to be best approached by examining and contrasting the plant genera *Metrosideros polymorpha* and *Acacia koa* (nonspeciating representatives) with the highly speciated genus *Cyrtandra*. Previous biochemical studies of *Metrosideros* (as reported in Technical Report No. 2, this series) found evidence for low levels of electrophoretic variability. These studies were complicated by several intrinsic factors, including:

(a) Comparatively low concentrations of protein material;
(b) The existence of high concentrations of plant phenols in *Metrosideros* which tended to disrupt electrophoretic banding patterns and lead to poor reproducibility; and
(c) Age dependent changes leading to difficulties in standardization of plant material.

Because of these factors, it became apparent that electrophoresis, as a genetic technique, would not be applicable to studying *Metrosideros* without some large investment of time and expense. It seemed appropriate, therefore, to investigate *Acacia koa* as to the feasibility of applying electrophoresis to this species.

Leaf samples of *Acacia*, *Styphelia* and *Dodonaea* were collected along the Mauna Loa strip road on the island of Hawaii by C. Corn. The material was analyzed in the lab of Dr. H. L. Carson at the University of Hawaii using methods previously described (Technical Report No. 2, this series). All species were electrophoresed simultaneously on the same gels along with greenhouse seedlings of *Metrosideros*. The following enzyme systems were analyzed: Phosphoglucose isomerase (pgi), phosphoglucomutase (pgm), alcohol dehydrogenase (adh), esterase (est), leucine aminopeptidase (lap), acid phosphatase (acph), indophenol oxidase (ipo), alpha-glycerophosphate dehydrogenase (alpha-gpdh) and malate dehydrogenase (mdh).

Koa showed good enzyme activity and banding for pgi, pgm, mdh, ipo, est, lap and acph. No activity was observed for alpha-gpdh and adh. *Dodonaea* stained for pgi, mdh, ipo, est and lap. On the other hand, *Styphelia* stained for mdh and lap and *Metrosideros* for pgi, mdh and lap only. The latter two genera showed poor band resolvement on the gels.

The koa samples were the only types to demonstrate electrophoretic variability between specimens. The proteins involved were pgm, pgi and acph. It is of interest to note that Dr. J. Brewbaker (personal communication) has recently found 2 polymorphic catalase systems in koa as well. This evidence suggests that koa may have levels of variability useful to the IBP study goals. Future studies are being planned to examine the extent of variation in koa and look for evidence of adaptation which may be reflected in clinal and ecotypic variation.

Acknowledgement: I wish to thank Carolyn Corn for the specimens utilized in these studies.

E-2

M. P. Mi
S. Yamashiro
K. Bridges
V. Carey

Progress report on data processing

The data processing activities continued in general support of the IBP Program. The results of this effort have not appeared separately, but are contained in the progress reports of the component projects.

In November, Sandy Yamashiro resigned from this project. Her considerable efforts, with the cooperation of M. P. Mi, were responsible for the establishment of many data-processing procedures, computer programs, and data decks. K. Bridges, with the assistance of V. Carey, are continuing this project.

It is expected that several technical reports will be issued as the direct result of the data-processing activities. Preparation of a report on the climate of the IBP transect and Kilauea Forest sites is underway. Another report will describe data-processing procedures for analyzing some standard ecological data, such as from weather station instruments. A third report will be a user's manual for a plotting program which will be made available for the use of the IBP participants.

7. TECHNICAL REPORT SERIES AND ABSTRACTS

7.1 - 7.10

7. TECHNICAL REPORT SERIES

ABSTRACTS

Mueller-Dombois, Dieter, ed. December 1970. Hawaii Terrestrial Biology Subprogram First Progress Report and Second-Year Budget. Technical Report No. 1. 144 pp.

Information on initiation of program, workshop meetings, strategy and development, plans for next year and supplemental information.

Mueller-Dombois, Dieter, ed. January 1972. Island Ecosystems Stability and Evolution Subprogram. Second Progress Report and Third-Year Budget. Technical Report No. 2. 290 pp.

Information of aims of program, workshop meetings, integration of research tasks, site coordination, progress of individual subprojects.

Spatz, Günter and D. Mueller-Dombois. February 1972. The influence of feral goats on koa (Acacia koa Gray) reproduction in Hawaii Volcanoes National Park. Technical Report No. 3. 16 pp.

Goats were introduced to the Hawaiian Islands nearly 200 years ago. They have become wild and today roam in many Hawaiian ecosystems with dry-season climates from the lowlands to the mountains. A quantitative analysis was made to evaluate the influence of feral goats on tree reproduction of Acacia koa in the mountain parkland ecosystem on the east flank of Mauna Loa. In this ecosystem, the endemic koa is the only important tree species. Here it reproduces vegetatively from root suckers. Suckering has resulted in the formation of small, dense tree colonies. Ten transects were established through a goat exclosure that was constructed three years earlier (in 1968). In addition, six transects were run across several typical nonfenced koa colonies. All suckers were counted, measured for height and mapped. It was shown that koa reproduction below 10 cm height is abundant outside the exclosure and at the unfenced colonies. Almost totally missing are suckers between 0.5 m and 2 m height. However, hundreds of this height grow inside the goat exclosure. Most of the few trees of this height found outside the fenced area were dying or dead showing that the current goat pressure is so high that the reproduction cycle of koa is nearly disrupted. The dense and vigorous sucker growth inside the exclosure, which is the result of current release from goat browsing pressure, was found to be an artifact. The artifact has resulted from increased suckering density caused by goat feeding and probably trampling on shallow roots. Thus, the entire forest stand structure in the mountain parkland is directly related to herbivore feeding and departs definitely in spacing and probably in height growth from the original forest structure as evolved during island ecosystem evolution.

Mueller-Dombois, Dieter. March 1972. A non-adapted vegetation interferes with soil water removal in a tropical rain forest area in Hawaii. Technical Report No. 4. 25 pp.

A bunch grass species (Andropogon virginicus) from the North American continent was introduced to the island of Oahu, Hawaii in 1932. The grass began to spread. Today it forms the dominant grass cover in the rain forest zone, wherever the trees have been removed. Grass dominance is maintained by accidental fires. The grass goes into dormancy during the winter months. At that time, the shoots dry up and the grass cover turns into a mulch of straw, with few green blades remaining active. Also at that time, rainfall increases. Tropical trees (Eugenia cuminii, Mangifera indica, Psidium gujava, a.o.) in the same area remain green and productive during the period of increased rainfall. Transpiration was compared for the tree cover and grass cover on a land area basis. It was found that the trees are able to recirculate the incoming rain water into the atmosphere, while the grass cover is unable to remove excess soil water between rain showers. This results in increased runoff, erosion and slumping of the soil under the grass cover. In addition to forming a poor utilizer of the water resources available for primary production, the introduced grass causes damage to the landscape. Reforestation and fire protection is the answer to this problem.

Gressitt, J. L. and C. J. Davis. April 1972. Seasonal occurrence and host-lists of Hawaiian Cerambycidae. Technical Report No. 5. 34 pp.

The cerambycid beetle borers play an important role in Hawaiian forests, both in the natural and disturbed environments. Their significance is enhanced by the disharmonic nature of the fauna, such as the lack of leaf beetles and june beetles in the native fauna. There are about 120 known species of endemic cerambycids, almost entirely restricted to native trees and shrubs, and 17 species of established exotic cerambycids, which with few exceptions bore in exotic trees. The seasonal occurrence, as far as known, of the adult cerambycids is tabulated. Altitudinal range and latest year of collection (native) or earliest year of record (exotic) are also tabulated. In a further tabulation, the species for which host associations are known are presented by host genera under plant families, and by islands. The introduced species are treated in similar manner.

Corn, Carolyn. August 1972. Seed dispersal methods in Hawaiian Metrosideros. Technical Report No. 6. 19 pp.

Hawaiian Metrosideros seeds need 3 to 12 miles per hour wind velocity to become airborne, and can survive -30°C temperatures for at least 6 hours. They also survive sea water soaking for 30 days followed by an additional 7 day desiccation period. These conditions substantiate a belief that Metrosideros species arrived in the islands by wind dispersal, and can also travel shorter distances by water currents.

Steffan, W. A. August 1972. Ecological studies of Ctenosciara hawaiiensis (Hardy) (Diptera: Sciaridae). Technical Report No. 7. 7 pp.

The seasonal fluctuations of Ctenosciara hawaiiensis (Hardy)populations in two different ecosystems at the same elevation on Mauna Loa on the island of Hawaii are compared and correlated with fluctuations in rainfall, humidity, and temperature. Rainfall appears to be the most important extrinsic factor affecting seasonal changes in this species. There is a marked difference between the two populations which in part could be explained by differences in the ecosystems. Ctenosciara hawaiiensis is closely associated with Acacia koa. The larvae live under the bark of dead branches.

Berger, A. J. August 1972. Birds of Hawaii Volcanoes National Park. Technical Report No. 8. 49 pp.

The dominant and subdominant plants are listed for 10 major vegetational and climatic areas within Volcanoes National Park. These areas are located at elevations between 1,400 and 10,000 feet. Information on the birds found in eight of the 10 areas during the late 1940s is available in the paper by Baldwin (1953); two of Baldwin's study plots are not included in the IBP transects, but data on the birds in these plots from 1970-72 are included in this report.

Notable differences between bird populations in the 1940s and the early 1970s are:

1. The apparent disappearance from the Park of two species of rare and endangered honeycreepers: Akiapolaau and Ou.

2. An apparent disappearance of the Apapane from certain low-elevation habitats.

3. A decrease in the range, and probably in population density, of the Elepaio.

4. The disappearance of the Hawaiian Thrush from at least two plots at low elevations.

5. A reversal in density of the Red-billed Leiothrix and the Japanese White-eye. The White-eye was first recorded in certain regions of the Park between 1940 and 1944. It now is found at nearly all levels and in all habitats within the Park from sea level to above tree line, and it is now the most common exotic species in the Park. The Red-billed Leiothrix is now common in suitable habitats,but population density probably is lower than during the 1940s.

6. The Hawaiian Goose now occurs regularly within Park boundaries, especially during the breeding season; the species was close to extinction during the 1940s and was not seen by Baldwin.

The discovery that the Apapane sometimes build nests in collapsed lava tubes is discussed. That this type of nesting behavior is not rare is suggested because it was found on Mt. Hualalai and at three widely separated sites on Mauna Loa.

At least three species of Plasmodium, the protozoan parasite that causes bird malaria, have been identified in the blood of one endemic (Apapane) and two introduced (Leiothrix and White-eye) species of birds in Volcanoes National Park. Studies on the mosquito vector for Plasmodium are needed.

Baldwin's (1953) thorough study of the insect food of the Amakihi, Apapane, and Iiwi is summarized, as is his discussion of the phenology of the tree species whose flowers provide nectar for the honeycreepers. The need for contemporary observations on the relationship of the Iiwi to lobeliad flowers is noted.

MacMillen, R. E. August 1972. Bioenergetics of Hawaiian honeycreepers: the Amakihi (Loxops virens) and the Anianiau (L. parva). Technical Report No. 9. 14 pp.

Bioenergetically the congeneric Hawaiian honeycreepers Loxops virens and L. parva are quite distinct from each other. L. virens has a higher T_B, lower and inconstant thermal conductance, and a standard metabolic rate (3.41 cm^3 O_2/g per hr) that is 96 per cent of that predicted for passerines. In L. parva, only about half the size of L. virens, standard metabolism (3.22 cm^3 O_2/g/hr) is lower than in the latter, and is reduced to 76 per cent of the predicted passerine level. Neither bird conforms to the Newtonian model of homeothermy, as L. virens has an inconstant thermal conductance below thermal neutrality, while in L. parva thermal conductance is constant but T_B is reduced at low T_A.

Evaporative water loss is rather comparable in both species, conforming closely to expected passerine levels in L. virens but considerably reduced below these levels in L. parva. Under conditions of high T_A, both species become hyperthermic and increase evaporative water loss, but insufficiently to dissipate by evaporation the heat that is produced metabolically, even under conditions of low atmospheric humidity. In four of six L. virens, T_A of ca. 39-40°C and T_B of 42.5-43.6°C proved fatal; L. parva was not exposed to such high T_A. High temperature tolerances apparently are lacking in these species, but they inhabit high forests where such temperatures are seldom encountered.

Smathers, G. A. and D. Mueller-Dombois. September 1972. Invasion and recovery of vegetation after a volcanic eruption in Hawaii. Technical Report No. 10. 172 pp.

A major volcanic eruption on the Island of Hawaii in December 1959 devasted an existing montane rain- and seasonal-forest covering an area of about 500 ha. The eruption resulted in a massive pahoehoe lava substrate on the crater floor of Kilauea Iki, in a new cinder cone, in an area covered with spatter and another with an extensive blanket of pumice varying along a fallout gradient from over 46 m to less than 2 cm deep. Six new habitats were recognized by kinds of substrate and remains of former vegetation. A study was made of plant invasion and recovery from the time of the disturbance till nine years thereafter. Plant records consisted primarily of periodically listing species by cover-abundance in a large number of quadrats along a transect system that crossed the crater floor and extended about 3 km along the fallout gradient. The atmospheric environment was studied concurrently by records of rainfall, lateral rain- and steam-interception and desiccating power. The substrates were examined for their

soil moisture properties, temperatures, mineralogical properties and available plant nutrients.

It was found that plants moved onto the crater floor within the first year. They progressed concentrically towards the crater center in correlation with a substrate-heat gradient that cooled progressively from the margin inward. Plant invasion on the cinder cone was delayed by 2 to 3 years, because of prolonged volcanic heating from below. A fast invasion took place on the spatter habitat where a surviving rain forest was nearby and where tree snags provided additional moisture locally at their base by intercepting wind-driven rains. Establishment at snag bases were also noted on the pumice, and generally, plant invasion occurred by aggregation of plants in favorable microhabitats which included crevices and tree molds. On the pumice, invasion progressed at a relatively uniform rate in spite of differences in substrate depth and atmospheric environment. The increase in plant cover was much faster on the habitats with vegetation remains than on those without. On the latter, the plant cover was still insignificant in year 9 after the eruption, in spite of a near total spread of plants across these habitats.

The sequence of life form establishment on substrates without vegetation remnants was clearly algae first, then mosses and ferns, then lichens, then native woody seed plants and finally exotic woody and herbaceous seed plants. On the substrates with former vegetation remains, exotic seed plants participated in the invasion process from the beginning. This was related to the availability of microhabitats with water relations favorable for plants with normal root systems and probably higher water requirements than the native sclerophyllous woody plants. A remarkable recovery occurred among Metrosideros polymorpha trees that were buried up to and over 2.5 m deep under pumice. Several native shrubs resprouted after their entire shoot system had been buried. The best herbaceous survivors were those with underground storage organs, which included both native and exotic species.

The invading exotics did in no way interfere with the establishment of the native pioneer plants. Initial stages of succession were observed whereby native woody plants began to replace exotic woody plants. Among herbaceous plants, exotic species were far more numerous, because there are only very few native species in this group. A succession, in part caused by competitive replacement, was noted among the exotic herbaceous plants. Thus, there appears to be no threat of native plants to be replaced by exotics on these new volcanic substrates. The native forms are better adapted to these harsh environments. But exotic complementary life forms are expected to remain in association with the native vegetation because of a lack of life forms among the native species to fill the available niches.

Berger, A. J. September 1972. Birds in the Kilauea Forest Reserve, a progress report. Technical Report No. 11. 22 pp.

The Kilauea Forest Reserve is notable for the island of Hawaii because it provides habitat for at least nine species of endemic birds, of which six species are members of the Hawaiian Honeycreeper family (Drepanididae): Amakihi, Akepa, Creeper, Akiapolaau, Apapane, and Iiwi. The other endemic species are the Hawaiian Hawk, the Elepaio, and the Hawaiian Thrush. The thrush is abundant throughout the forest, and is common even in areas that

have been disturbed by cattle and by logging operations.

Two species of introduced birds occur in relatively large numbers: Japanese White-eye and Red-billed Leiothrix. Other species of introduced birds are found in the pasture land adjacent to the forest but have not been seen within the forest itself.

The foraging behavior of endemic and introduced species is discussed. No data are available to suggest that introduced species compete with endemic birds for food or for nesting sites.

Nesting data are presented. An apparently unusual feature about the Apapane is that this species not uncommonly builds its nest on the tops of tree fern fronds, rather than in ohia trees, which is the typical site for nests of this species in ohia-tree fern forests.

The adaptability of three endemic species (Elepaio, Amakihi, Akiapolaau) and two introduced species (Japanese White-eye, Red-billed Leiothrix) to wide vegetational and climatic conditions is discussed. Physiological data obtained by Dr. Richard E. MacMillen on captive Amakihi from Hawaii and Kauai are presented.

Paik, Y. K. and K. C. Sung. February 1973. Ecogeographical variations of chromosomal polymorphism in Hawaiian populations of Drosophila immigrans. Technical Report No. 12. 25 pp.

Eighteen samples from twelve populations of Drosophila immigrans in the islands of Kauai, Oahu and Hawaii in the Hawaiian archipelago were analyzed for inversion polymorphism in 1125 females and 206 males. Three kinds of second chromosome inversions, which appear to be identical with those previously reported by other workers, were present in all of our populations; two other new inversions of the same autosome were detected from the Hawaii collections, but their origin, whether natural or laboratory, could not be assured.

The average proportions of inversion heterozygosity per individual of the populations from Kauai, Oahu and Hawaii was about 34%, 32% and 65% respectively. The frequencies of heterozygous inversions were similar between different populations within islands (with one notable exception on Hawaii). In contrast, the frequencies were significantly heterogeneous from one island to the next. The results of gene arrangement frequency analysis consolidated the above findings. It is suggested that the inter-island differentiations are due to natural selection and probably maintained by the isolation by oceanic channels. Two near-by localities on Hawaii were inhabited with significantly heterogeneous populations. Such a microgeographic differentiation has been interpreted as being due to the presence of highly localized, differential selection forces in the two localities, and the difference seems to be maintained due to isolation by the lava flows.

Our data suggest that the breeding units of Hawaiian populations of D. immigrans are not so small as to allow for genetic drift to significantly affect the populations. Inversion polymorphism was similar between females and males taken at the same time in the same localities.

Mueller-Dombois, D. and G. Spatz. October 1972. The influence of feral goats on the lowland vegetation in Hawaii Volcanoes National Park. Technical Report No. 13. 46 pp.

The coastal lowland of Hawaii Volcanoes National Park, particularly its western part, is a concentration center of feral goats. Here, in a tropical seasonal climate, a widespread vegetation is an annual Eragrostis tenella grassland that occurs on lava rock substrates with thin layers of ash. Localized within this area occurs also a small area of deep-ash deposit (Puu Kaone) that is occupied by perennial introduced grass with scrub.

Experimental goat displacement in form of exclosures on these two grasslands has shown that both are entirely goat-derived vegetations. The response to displacement of goats was immediate in both areas. In the annual grassland, bunchgrasses, woody chamaephytes and an endemic legume vine (Canavalia kauensis) became established within less than two years, while the annuals are fast disappearing. In the perennial grassland, Melinis minutiflora enlarged its grass mat, woody plants became more abundant and exposed soil was partially covered within a year after exclosure construction.

The remarkable recovery of the endemic vine in the annual grassland shows that goat removal still holds hopes for at least a partial return of native vegetation. The effects of goats apart from their physical degradation of the lowland ecosystem has been primarily in the form of exhausting the seed supply of native plants by feeding on seedlings wherever they occurred in this territory. Total elimination of goats from this area can be expected to yield a partial return of native plants on these rockland surfaces.

Mueller-Dombois, D. and G. Spatz. October 1972. The influence of SO_2 fuming on the vegetation surrounding the Kahe Power Plant on Oahu, Hawaii. Technical Report No. 14. 12 pp.

The study relates to an investigation of the vegetation around Kahe power station, a recently established electricity generating plant at Kahe Point on SW Oahu. A vegetation map was prepared from aerial photographs at 1 : 5,000 and a search was made for possible SO_2 damage manifestations from the fumes emitted by the plant. Three major communities were identified, (1) closed forest of Prosopis pallida, (2) open forest-scrub dominated by Leucaena leucocephala and Acacia farnesiana and (3) open scrub-grassland dominated by the native pili grass (Heteropogon contortus). Within each of these major units, two to three floristic and structural subunits were mapped. No SO_2 damage was noted in the vascular plants. A separate survey of rock-lichens on identically sea-breeze-exposed ridges, north and south of the power plant, showed a considerably lower abundance of foliose rock-lichens in the southern area which receives much of the SO_2 plume. It was concluded that a beginning influence is shown by the lower abundance of lichens and that SO_2 damage in the vascular plants may show up only during the rainy season when the vegetation is actively growing. The investigation was done during the dry season in September.

Spatz, G. and D. Mueller-Dombois. November 1972. Succession patterns after pig digging in grassland communities on Mauna Loa, Hawaii. Technical Report No. 15. 22 pp. + 12 Appendices.

The influence of feral pigs on the composition of grassland communities on the east flank of Mauna Loa, Hawaii, was studied for the one year period from July, 1971 to August, 1972. Actual pig-disturbed areas as well as artificially scalped plots were included in the study. The succession on those plots was measured by both frequency and cover measurements.

It was found that pig digging greatly enlarges the component of introduced species in communities with a former high percentage of native species.

Howarth, F. G. December 1972. Ecological studies on Hawaiian lava tubes. Technical Report No. 16. 20 pp.

The Hawaiian Islands offer great potential for evolutionary research. The discovery of specialized cavernicoles among the adaptively radiating fauna adds to that potential. About 50 lava tubes and a few other types of caves on 4 islands have been investigated. Tree roots, both living and dead, are the main energy source in the caves. Some organic material percolates into the cave through cracks associated with the roots. Cave slimes and accidentals also supply some nutrients. Lava tubes form almost exclusively in pahoehoe basalt, usually by the crusfing over of lava rivers. However, the formation can be quite complex. Young basalt has numerous avenues such as vesicles, fissures, layers, and smaller tubes which allow some intercave and interlava flow dispersal of cavernicoles. In older flows these avenues are plugged by siltation or blocked or cut by erosion.

Spatz, Günter O. February 1973. Some findings on vegetative and sexual reproduction of koa. Technical Report No. 17.

Some environmental factors which influence the reproductive behavior of Acacia koa var. hawaiiensis (Rock) were studied on the east flank of Mauna Loa, Hawaii. Additionally, some factors were tested under controlled conditions.

It was found that soil moisture as well as soil temperature in terms of day-degrees are limiting factors for koa germination. Variability among individual seeds in regard to their germination requirements is very high. This results in a functional relationship between germination rates and time. The gases in the seed bed seem to be important factors influencing germination, as indicated by the stimulating effect of soil cultivation. Dry periods limit survival of germinated seeds.

Vegetative suckering is a compensative reproductive behavior in drier and/or cooler areas. But suckering does not occur when the soil is covered by a dense and tall grass sward. Scalping the sward, and to a smaller degree, clipping of the vegetation, stimulates koa suckering.

Initial growth in suckers and seedlings depends on temperature, soil moisture and light intensity. It was possible to show some relationships quantitatively.

Corn, Carolyn and William Hiesey. February 1973. Altitudinal ecotypes in Hawaiian Metrosideros. Technical Report No. 18.

Hawaiian Metrosideros distribution extends from tropical to cool-temperature climates throughout the six major islands of the Hawaiian Island chain. It forms a highly polymorphic complex that occurs in a continuous distribution over areas with average annual rainfalls ranging from 30 to 450 inches and at elevations from sea-level to 8500 feet, and in diverse pedological and topographical habitats. All of these plants are probably derived from one or a very small number of ancestral introductions that arrived within the last 20 million years by long-distance dispersal.

Seeds collected from diverse altitudinal sites on the islands of Hawaii and Maui and grown under uniform greenhouse conditions show evidence of ecotypic differentiation along altitudinal gradients. The seedlings, although from islands separated by 50 miles of ocean, show a parallelism in their altitudinal intra-population variation that strongly overlaps from site to site.

Mueller-Dombois, Dieter. February 1973. Some aspects of island ecosystems analysis. Technical Report No. 19. 26 pp.

The point is made that ecological principles generated from the study of continental ecosystems cannot be extrapolated to oceanic islands without reservations. Island ecosystems are not necessarily unique at the level of biome or formation structure, but they differ greatly at the level of life form and species structure, and as such, they differ also in their functional and dynamic relations. The greatest departure occurs in the area of species interaction. Examples of such departures are given in three areas of ecosystem analysis:

(1) Spatial distribution of island biota,
(2) Niche differentiation, and
(3) Successional phenomena.

The differences in ecological relationships of oceanic island ecosystems are a direct reflection of their special biological evolution, caused by geographic isolation, small habitat size and recent geological age. Perhaps more so than elsewhere, ecosystem analysis on islands cannot be meaningful without an appreciation of their special evolutionary relationships. However, to some extent this applies also when trying to extrapolate results of ecosystem analysis from one biogeographic region to another. It is suggested that the ecological consequences of different biological evolutions are best recognized by studying ecologically similar species within the context of their general niches and by relating these to the ecosystem as a whole.

8. LIST OF CONTRIBUTIONS AND THESES

8.1 - 8.4

ISLAND ECOSYSTEMS IRP/IBP HAWAII

Contributions

#1 Howarth, F. G. 1971. Cavernicoles in lava tubes on the island of Hawaii. Science 175: 325-326.

#2 Mi, M. P., S. Yamashiro and D. Mueller-Dombois. 1972. Data storage and retrieval for the study of Hawaiian ecosystems. Proc. Fifth Hawaii Intern. Confer. on Systems Sciences

#3 Gressitt, J. L. and C. J. Davis. 1971. New plagithmysines from Kauai, Molokai and Hawaii. Proc. Hawaiian Ent. Soc. 21(1): 67-77.

#4 Gressitt, J. L. 1972. New plagithmysines from Molokai, Lanai and Maui. Pacific Insects 14(1): 83-92.

#5 Gressitt, J. L. and C. J. Davis. 1972. Seasonal occurrence of the Hawaiian Cerambycidae (Col.). Proc. Hawaiian Ent. Soc. 21(2): 213-221.

#6 Spatz, GÜnter and D. Mueller-Dombois. In press. The influence of feral goats on koa tree reproduction in Hawaii Volcanoes National Park. Ecology.

#7 Mueller-Dombois, D. A non-adapted vegetation interferes with soil water removal in a tropical rain forest area in Hawaii. Submitted for publication.

#8 Corn, Carolyn. 1972. Seed dispersal methods in Hawaiian Metrosideros. In John A. Behnke, (ed.). Challenging Biological Problems. Oxford University Press, N. Y. 200 pp.

#9 Gressitt, J. L. 1972. New plagithmysines from West Maui (Col.: Cerambyc.) Pacific Insects 14(4): 635-645.

#10 Gressitt, J. L. and Clifton J. Davis. 1972. Seasonal occurrence and host-lists of Hawaiian Cerambycidae. Proc. of Hawaiian Ent. Soc. 21(3).

#11 Fennah, R. G. In press. The cavernicolous fauna of Hawaiian lava tubes. Part IV. Two new species of Oliarus (Fulgoroidae: Cixiidae). Pacific Insects 15(1).

#12 MacMillen, Richard E. In press. Bioenergetics of Hawaiian honeycreepers: the Amakihi (Loxops virens) and the Anianiau (L. parva). Condor.

#13 Holbrook-Walker, S. and R. M. Lloyd. In press. Reproductive biology and gametophyte morphology of the Hawaiian fern genus Sadleria (Blechnaceae) relative to habitat diversity and propensity for colonization. Bot. J. of the Linnean Society.

#14 Steffan, Wallace. In press. Ecological studies of Ctenosciara hawaiiensis (Hardy) (Diptera: Sciaridae). Pacific Insects.

#15 Paik, Y. K. and Kee Chang Sung. Ecogeographical variations of chromosomal polymorphism in Hawaiian populations of Drosophila immigrans. Submitted for publication.

#16 Corn, Carolyn and William Hiesey. In press. Altitudinal ecotypes in Hawaiian Metrosideros. Amer. Journal of Botany.

#17 Howarth, F. G. In press. The cavernicolous fauna of Hawaiian lava tubes. Part I. Introduction. Pacific Insects 15(1).

#18 Gertsch, Willis J. In press. The cavernicolous fauna of Hawaiian lava tubes. Part III. Araneae (spiders). Pacific Insects 15(1).

#19 Schultz, George A. In press. The cavernicolous fauna of Hawaiian lava tubes. Part II. Isopoda (Crustacea). Pacific Insects 15(1).

#20 Steffan, Wallace. In press. Redescription of Bradysia tritici and B. reynoldsi. Proc. of Hawaiian Ent. Soc.

#21 Gressitt, J. L. and C. J. Davis. In press. Two new plagithmysines from Maui and Hawaii (Col.: Cerambycidae). Proc. of Hawaiian Ent. Soc.

#22 Mueller-Dombois, D. Some aspects of island ecosystems analysis. Submitted for publication.

#23 Hardy, D. Elmo and Mercedes D. Delfinado. Flightless Dolichopodidae (Diptera) in Hawaii. Submitted for publication.

Theses prepared under partial support of the US/IBP ISLAND ECOSYSTEMS IRP. The titles and completion dates of expected theses are tentative. All programs are associated with the University of Hawaii unless otherwise noted.

Becker, R. E. The competitive capacity of Hawaiian tree ferns. Ph.D., expected Spring 1975.

Brennan, B. M. Aspects of the biology of a tachinid parasite. Ph.D., expected December 1974.

Brown, William Y. Breeding biology and factors in breeding success of some tropical terns. Ph.D., expected June 1973.

Carson, Johnny L. Microbial ecology of Hawaiian Islands. Ph.D., expected 1973, University of North Carolina.

Conant, Michael. Nuclear polyhedrosis of Uresiphita polygonalis. M.S., expected June 1973.

Cooray, R. G. Tree population structure of a montane rain forest on Mauna Loa, Hawaii. M.S., expected June 1973.

Cooray, R. G. The impact of feral pigs on the Hawaiian rain forest. Ph.D., expected June 1976.

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Eddinger, C. Robert. A study of the breeding biology of four species of Hawaiian honeycreepers (Drepanididae). Ph.D., December 1970.

Gagne, Wayne. Insular evolution and speciation of the genus Nesiomiris Kirkaldy (Heteroptera: Miridae) in the Hawaiian Islands. Ph.D., expected September 1973, University of California, Berkeley.

Guest, Sandra. Breeding biology of the Japanese White-eye (Zosterops japonica). M.S., expected August 1973.

Hirai, Lawrence. Breeding biology of the house finch (Carpodacus mexicanus). M.S., expected August 1973.

Howarth, F. G. Biology and systematics of the Culicoides of Laos (Diptera: Ceratopagonidae). Ph.D., expected December 1973.

Karganilla, Nelda. Edaphic algae of Hawaii Volcanoes National Park. M.S., August 1972.

Lee, B. K. H. Ecological and physiological studies of soil microfungi in Heeia mangrove swamp, Oahu, Hawaii. Ph.D., May 1971.

Leeper, John R. Bioecology of the Acacia psyllid in Hawaii. Ph.D., expected June 1975.

Maka, Jean. Spatial pattern analysis of plant synusiae in a montane rain forest on Mauna Loa, Hawaii. M.S., expected June 1973.

McGurk, Linda-Lee. Algal distribution in Hawaii Volcanoes National Park in relation to various environmental factors. M.S., expected August 1973.

Meeker, Joseph A. Atichia in Hawaii. Ph.D., expected August 1973.

Nakahara, Larry. Distribution and abundance of psyllids on Metrosideros on Mauna Loa, Hawaii. M.S., expected August 1973.

Porter, John R. The growth and phenology of Metrosideros in Hawaii. Ph.D., September 1972.

Smathers, G. A. Invasion, early succession and recovery of vegetation on the 1959 Kilauea volcanic surfaces, Hawaii Volcanoes National Park, Hawaii. Ph.D., August 1972.

Spatz, G. O. Comparative analysis of pasture and tree production on a tropical montane rain forest habitat, Hawaii. Habilitation for professorship, expected June 1974, Tech. Univ., Munich.

Steiner, W. W. M. Species relationships and genotype-environment interactions in selected species of the Hawaiian Drosophilidae. Ph.D., expected August 1974.

Sung, Kee Chang. Selection of inversions in Hawaiian populations of Drosophila immigrans. Ph.D., expected December 1973.

Tenorio, J. Taxonomic and biological studies of Hawaiian Ephydridae (Diptera). Ph.D., May 1971.

Van Riper, Charles. Comparative breeding biology of four species of Hawaiian honeycreeper (Drepanididae) on the island of Hawaii. Ph.D., expected June 1974.

Wirawan, N. Floristic and structural development of native dry forest stands at Mokuleia, NW Oahu. M.S., May 1972.

Wirawan, N. Effect of vegetation cover on soil-water relations in a tropical rain forest area, Hawaii. Ph.D., expected June 1975.

9. BUDGET FOR FY 74 and FY 75

9.1 - 9.49

Proposed IBP Grant Budget, 04 Year, 1973-74

BUDGET SUMMARY

	Requested from NSF	Institution Contribution
I. UNIVERSITY OF HAWAII	$326,550	$27,970
II. B. P. BISHOP MUSEUM	$147,400	*
TOTAL REQUESTED	$473,950	$27,970

* THE BISHOP MUSEUM WILL COST-SHARE IN ACCORDANCE WITH CURRENT NATIONAL SCIENCE FOUNDATION POLICY (NSF NOTICE NO. 31, DATED 9-3-70)

Proposed IBP Grant Budget, 04 Year, 1973-74
University of Hawaii

SUMMARY

	NSF Funded Man Months Cal/Acad/Sum			UH Funded Man Months Cal/Acad/Sum			PROPOSED NSF	PROPOSED UH
A. SALARIES AND WAGES								
1. Principal Investigator & Faculty Associates								
2 Co-Principal Investigators		5	4				19,044	
13 Senior Personnel	21	5	6	6	5		43,639	23,191
Subtotal							62,683	23,191
2. Other Personnel								
Asst. & Assoc. Researchers	24						21,660	
Technicians	24						14,877	
Graduate Assistants	78						65,484	
Student help							6,900	
Subtotal							108,921	
Total Salaries and Wages							171,604	23,191
B. FRINGE BENEFITS							20,034	4,779
Total Salaries, Wages and Fringe Benefits							191,638	27,970
C. PERMANENT EQUIPMENT							3,483	
D. EXPENDABLE SUPPLIES AND EQUIPMENT							11,050	
E. TRAVEL								
1. Domestic							18,456	
2. International								
Total Travel							18,456	
F. PUBLICATION COSTS							5,950	
G. OTHER COSTS							17,034	
H. TOTAL DIRECT COSTS							247,611	27,970
I. INDIRECT COSTS								
1. On-campus 46.00% of Salaries & Wages ($171,604)							78,939	
J. TOTAL COSTS							$326,550	$27,970

Proposed IBP Grant Budget, 04 Year, 1973-74
B. P. Bishop Museum

BUDGET SUMMARY

	NSF Funded Man Months Cal/Acad/Sum	BM Funded Man Mohths Cal/Acad/Sum	PROPOSED NSF	PROPOSED BM
A. SALARIES AND WAGES				
1. Principal Investigators & Res. Assoc.				
Co-Principal Investigator		1	2,400	
5 Senior Personnel	22	2	24,657	
Sub-Total			27,057	
2. Other Personnel				
5 Technicians	39		19,350	
2 Field/Lab. Asst.	12		7,750	
1 Plant Identifier	6		4,000	
1 Computer Operator	12		7,896	
1 Maintenance Man	12		7,200	
1 Admin. Asst/Secretary	12		7,600	
Sub-Total			53,796	
Total Salaries and Wages			80,853	
B. FRINGE BENEFITS			6,207	
Total Salaries, Wages & Fringe Benefits			87,060	
C. PERMANENT EQUIPMENT			2,500	
D. EXPENDABLE EQUIPMENT AND SUPPLIES			960	
E. TRAVEL (Domestic)			5,650	
F. PUBLICATION			400	
G. OTHER COSTS			5,100	
H. TOTAL DIRECT COSTS			101,670	
I. INDIRECT COSTS				
1. On-Campus 56.56% of Salaries & Wages ($80,853)			45,730	
J. TOTAL COSTS			$147,400	

THE BISHOP MUSEUM WILL COST-SHARE IN ACCORDANCE WITH CURRENT FOUNDATION POLICY.

Proposed IBP Grant Budget, 04 Year, 1973-74
B. P. Bishop Museum

Section: Entomology
Investigator: J. L. Gressitt
Project Code & Title: C-3(a), Hawaiian Cerambycid Beetles and Certain Other Woodborers

	NSF Funded Man Months Cal/Acad/Sum	BM Funded Man Months Cal/Acad/Sum	PROPOSED NSF	PROPOSED BM
A. SALARIES AND WAGES				
1. Principal Investigator & Res. Assoc. J. L. Gressitt, Entomologist; C. J. Davis, Res. Assoc.; G. A. Samuelson, Res. Assoc. (Boring insects; identifications)	1		2,400	
Subtotal			2,400	
2. Other Personnel				
Field and Lab. Asst.	6		4,400	
Lab Technician	3		1,450	
Subtotal			5,850	
Total Salaries and Wages			8,250	
B. FRINGE BENEFITS			660	
Total Salaries, Wages & Fringe Benefits			8,910	
C. PERMANENT EQUIPMENT				
Insect cases for storage			300	
D. EXPENDABLE SUPPLIES AND EQUIPMENT				
Nets, sleeve cages, traps, nutrient media, chemicals, vials, tubes, misc.			300	
E. TRAVEL				
1. Domestic Inter-island travel (airfares, per diem, vehicle rental)			1,200	
F. PUBLICATION COSTS			100	
G. OTHER COSTS				
H. TOTAL DIRECT COSTS			10,810	
I. INDIRECT COSTS				
1. On-campus 56.56% of Salaries & Wages ($8,250)			4,666	
J. TOTAL COSTS			$15,476	

THE BISHOP MUSEUM WILL COST-SHARE IN ACCORDANCE WITH CURRENT FOUNDATION POLICY.

Proposed IBP Grant Budget, 05 Year, 1974-75

BUDGET SUMMARY

	Requested from NSF	Institution Contribution
I. UNIVERSITY OF HAWAII	$302,903	$23,298
II. B. P. BISHOP MUSEUM	$156,504	*
TOTAL REQUESTED	$459,407	$23,298

* THE BISHOP MUSEUM WILL COST-SHARE IN ACCORDANCE WITH CURRENT NATIONAL SCIENCE FOUNDATION POLICY (NSF NOTICE NO. 31, DATED 9-3-70)

Proposed IBP Grant Budget, 05 Year, 1974-75
University of Hawaii

SUMMARY

	NSF Funded Man Months Cal/Acad/Sum	UH Funded Man Months Cal/Acad/Sum	PROPOSED NSF	PROPOSED UH
A. SALARIES AND WAGES				
1. Principal Investigator & Faculty Associates				
2 Co-Principal Investigators	5 4		19,776	
10 Senior Personnel	12 5 6	4 5	34,154	19,324
Subtotal			53,930	19,324
2. Other Personnel				
Asst. & Assoc. Researchers	24		22,524	
Technicians	24		15,492	
Graduate Assistants	78		67,164	
Student help			5,700	
Subtotal			110,880	
Total Salaries and Wages			164,810	19,324
B. FRINGE BENEFITS			18,260	3,974
Total Salaries, Wages and Fringe Benefits			183,070	23,298
C. PERMANENT EQUIPMENT			1,400	
D. EXPENDABLE SUPPLIES AND EQUIPMENT			9,750	
E. TRAVEL				
1. Domestic			15,656	
2. International				
Total Travel			15,656	
F. PUBLICATION COSTS			6,150	
G. OTHER COSTS			11,066	
H. TOTAL DIRECT COSTS			227,092	23,298
I. INDIRECT COSTS				
1. On-campus 46.00% of Salaries & Wages ($164,810)			75,811	
J. TOTAL COSTS			$302,903	$23,298

Proposed IBP Grant Budget, 05 Year, 1974-75
B. P. Bishop Museum

BUDGET SUMMARY

	NSF Funded Man Months Cal/Acad/Sum	BM Funded Man Months Cal/Acad/Sum	PROPOSED NSF	PROPOSED BM
A. SALARIES AND WAGES				
1. Principal Investigators & Res. Assoc.				
Co-Principal Investigator		1	2,500	
5 Senior Personnel	22	2	28,282	
Sub-Total			30,782	
2. Other Personnel				
5 Technicians	39		20,600	
2 Field/Lab. Asst.	12		8,400	
1 Plant Identifier	6		4,100	
1 Computer Operator	12		8,208	
1 Maintenance Man	12		7,500	
1 Admin. Asst./Secretary	12		7,900	
Sub-Total			56,708	
Total Salaries and Wages			87,490	
B. FRINGE BENEFITS			6,720	
Total Salaries, Wages & Fringe Benefits			94,210	
C. PERMANENT EQUIPMENT			500	
D. EXPENDABLE EQUIPMENT AND SUPPLIES			1,010	
E. TRAVEL (Domestic)			5,100	
F. PUBLICATION			1,100	
G. OTHER COSTS			5,100	
H. TOTAL DIRECT COSTS			107,020	
I. INDIRECT COSTS				
1. On-Campus 56.56% of Salaries & Wages ($87,490)			49,484	
J. TOTAL COSTS			$156,504	

THE BISHOP MUSEUM WILL COST-SHARE IN ACCORDANCE WITH CURRENT FOUNDATION POLICY.

Proposed IBP Grant Budget, 05 Year, 1974-75
B. P. Bishop Museum

Section: Entomology
Investigator: J. L. Gressitt
Project Code & Title: C-3(a), Hawaiian Cerambycid Beetles and Certain Other Woodborers

	NSF Funded Man Months Cal/Acad/Sum	BM Funded Man Months Cal/Acad/Sum	PROPOSED NSF	PROPOSED BM
A. SALARIES AND WAGES				
1. Principal Investigator & Res. Assoc. J. L. Gressitt, Entomologist; C. J. Davis, Res. Assoc.; G. A. Samuelson, Res. Assoc. (Boring insects; identifications)	1		2,500	
Subtotal			2,500	
2. Other Personnel				
Field and Lab. Asst.	6		4,800	
Lab Technician	3		1,600	
Subtotal			6,400	
Total Salaries and Wages			8,900	
B. FRINGE BENEFITS			712	
Total Salaries, Wages and Fringe Benefits			9,612	
C. PERMANENT EQUIPMENT Insect cases for storage			300	
D. EXPENDABLE SUPPLIES AND EQUIPMENT Nets, sleeve cages, traps, nutrient media, chemicals, vials, tubes, misc.			300	
E. TRAVEL				
1. Domestic Inter-island travel (airfares, per diem, vehicle rental)			1,200	
F. PUBLICATION COSTS			200	
G. OTHER COSTS				
H. TOTAL DIRECT COSTS			11,612	
I. INDIRECT COSTS 1. On-campus 56.56% of Salaries & Wages ($8,900)			5,034	
J. TOTAL COSTS			$16,646	

THE BISHOP MUSEUM WILL COST-SHARE IN ACCORDANCE WITH CURRENT FOUNDATION POLICY.

10. LITERATURE CITED

10.1 - 10.3

10. LITERATURE CITED

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NOTE: References cited in synthesis sections 2 through 5 but not contained in the above listing indicates unpublished meeting reports; copies are available on request.

March 15, 1973

MEMORANDUM

TO: ISLAND ECOSYSTEMS IRP Participants

FROM: Dieter Mueller-Dombois

SUBJECT: Next workshop meeting, April 6, 1973, 1:30-5:30 p.m. (Place will be designated with the Agenda, which will follow shortly.)

1. The purpose of this workshop meeting will be to evaluate our current status as an integrated project. Please reserve this Friday afternoon. It will be an important meeting. See further details below.

2. The THIRD PROGRESS REPORT AND BUDGET PROPOSAL FOR FY 74 and FY 75 (Tech. Report #21) has been completed and was hand-carried today to the U.H. Research Administration. Twenty copies will be airmailed to NSF within the next few days. Our NSF deadline is April 1.

3. Copies with budget summaries but without the detailed budgets are now being collated and you can expect your copy of Tech. Report #21 within a few days. Your own two budget sheets for FY 74 and FY 75 will be added in loose-leaf.

4. Please take the time to read Chapters 1 through 5. The ideas presented in these chapters should guide our integration efforts for the final year of operation under the IBP label. Continuation plans beyond the IBP deadline (June 1974) are detailed in the INTRODUCTION. Please take particular note of TABLE 1 (p. 1.3) which shows seven current and future activity areas with proposed target dates. We will discuss these areas and plans at the April 6 meeting.

5. The meeting will be an informal "round-table" discussion on our goals and priorities during the coming summer and the IBP synthesis phase. Please reserve the whole afternoon. The main discussion themes will be our three ecosystem analysis themes: (1) Spatial distribution of island biota, (2) Temporal phenomena in island ecosystems and (3) Niche differentiation. Theme 4 (Genetic variation within species) is well circumscribed by Hampton L. Carson in Tech. Report #21, and does not seem to constitute a major problem in integration.

6. An agenda for the April 6 meeting will follow shortly.